Synchronous species responses reveal phenological guilds: implications for management

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Abstract. Phenological studies are critical for understanding the ability of terrestrial ecosystems to respond to changes in climate. Monitoring seasonal transitions at the species or community level across large areas is challenging and expensive. One approach for lowering costs is to identify phenological guilds—groups of species that exhibit similar timing of seasonal transitions—and limit monitoring to a smaller number of species within a guild. In this study, we evaluated 23 consecutive years of monthly observations of individual species at 15 long-term study sites at the Jornada Basin USDA-Long-Term Ecological Research site to identify patterns in the onset of three phenophases—leaf-out, flower, and fruit—of 16 widely occurring species in the arid southwestern United States and to investigate the existence of phenological guilds. We conducted univariate analyses of distributions in the timing of leaf, flower, and fruit production across time and space and multivariate cluster analysis of the time series to identify coherent groups of species–site instances that exhibit coherence in timing of phenophase onsets (i.e., guilds). The six species of C_3 shrubs demonstrated greater consistency in timing of all phenophases relative to C_4 grasses. Further, we found that in all species, leaf-out occurred prior to the onset of the summer monsoon rains. Cluster analysis revealed six groups of species–site observations demonstrating high within-year concordance in timing of leaf-out and first fruit across variable site conditions and rainfall years. The six groups for timing of first fruit differed from those for first leaf in that they exhibited greater multi-species membership and within-year variability in timing. We propose that use of phenological guilds can improve the efficiency of ecosystem monitoring, predictive models of ecosystem cues driving phenological events, and land management outcomes.

Key words: Chihuahuan Desert; drylands; first fruit; first leaf; Long-Term Ecological Research; pattern recognition; phenological functional group; plant phenology; Special Feature: Dynamic Deserts; start of season.

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INTRODUCTION

In an era of changing climatic conditions, reliable and timely phenology information is increasingly important (Morisette et al. 2009, Richardson et al. 2013). A greater understanding of phenology—the timing of seasonal events in plants and animals—as well as the conditions that drive species-level phenological transitions such as leaf-out or migration, is important to forecast and evaluate outcomes of management decisions that influence agricultural production, habitat for sensitive species, and myriad ecosystem services. Plant phenology influences both storage and uptake of carbon, land–atmosphere interactions, surface hydrology, and important ecosystem services such as pollination (Parmesan and Yohe 2003, Sherry et al. 2007, Richardson et al. 2013). Recognition of phenology as an integrative metric of ecosystem response to climate is evident as a growing field of study (Donnelly and Yu 2017), but application of new knowledge gained to inform management and decision-making is slow to follow pace (Enquist et al. 2014). We aim to strengthen links between phenology, resource management, and decision-making with a long-term perspective on desert plant phenology.

Data documenting seasonal transitions are collected at temporal and spatial scales corresponding to plant species up to the biome as a whole (Morisette et al. 2009). Phenology patterns at the level of plant species and plant communities are most relevant for making actionable natural resource management decisions (Enquist et al. 2014). Data corresponding to plant species and community levels are clearly related in that species-level phenological information is the basis for understanding community-level responses to climate or management. Yet, data needs for specific management applications vary. Species-level phenology can inform natural resource management decisions such as timing the application of herbicides to target invasive species, optimizing water allocations for crop rotations to sustainably increase agricultural production, and managing livestock to more equitably distribute grazing pressure in large pastures with spatially and temporally variable forage production (Enquist et al. 2014, Wheeler et al. 2015, Browning et al. 2018). Knowledge of species phenology can serve as a basis for identifying groups of species or landscape elements that exhibit similar patterns in the timing and distribution of phenophases.

The ability to identify groups of species or landscape elements that exhibit similar responses to biotic or abiotic drivers can increase efficiency of monitoring efforts to characterize ecosystem responses to perturbation, climate, or changing management practices (Rosenfeld 2002, Gurevitch et al. 2006). Such groupings of species that exhibit similar patterns in the timing of seasonal transitions, or phenological guilds, can also be used in restoration efforts to choose an appropriate combination of plant species in seed mixes or to improve the timing of restoration implementation (e.g., following disturbance from oil and gas drilling or mining operations; Buisson et al. 2017). Further, an awareness of phenological guilds may also expand our understanding of functional responses to climate when linked to the underpinning mechanisms via experimental manipulations.

Compared to temperate systems, the phenology of arid and semi-arid systems is much less studied (Primack and Miller-Rushing 2011, Wolkovich and Cleland 2011), even though drylands occupy 41% the surface of the Earth (MEA 2005). Water-limited systems are generally characterized by high inter-annual variability in precipitation and soil moisture (Duniway et al. 2018). Therefore, it is especially important to evaluate plant responses in these systems using long-term studies and when possible, to examine patterns in the context of plant available water (PAW). Precipitation, air temperature, soil texture, and landscape position interactions are known to influence plant available soil moisture and plant phenology in arid and semi-arid systems (Pavon and Briones 2001, Seghieri et al. 2009, Kurc and Benton 2010, Cardoso et al. 2012). Species included in this study are widely distributed perennial components of plant communities in the arid and semi-arid Basin and Range Province of the United States and encapsulate two plant growth forms (C_3 and C_4) that differ in seasonality, rooting depth, and photosynthetic pathway (Syvertsen et al. 1976, Gibbens et al. 2005). Species are found at sites that occur on a range of soil types differing in landscape position, texture, and depth (Huenneke et al. 2002, Peters et al. 2012).

In this study, we used a long-term dataset from a water-limited system to test the potential for

grouping species by phenological guilds and to enhance our basic understanding of plant phenology throughout the growing season. Our first objective was to evaluate consistency in timing of leaf-out, flowering, and fruiting onsets for each of six C_3 shrub and ten C_4 grass species across sites and years. Given the range in site conditions and wet and dry years in the study period, we anticipated that species with deeper rooting systems (C_3 shrubs) would exhibit less variability in timing of initial growth (narrower distributions in timing) than species with shallower rooting systems (C_4 grasses). In addition, we anticipated that timing of initial growth (first leaf) would be more variable than reproductive phenophases (i.e., first flower or fruit). Our second objective was to identify phenological guilds, defined here as groups of species that demonstrate coherence in start time of leafing, flowering, or fruiting, over the 23-yr study period. We anticipated both that clear guilds would emerge and that the groupings of species into guilds would be consistent across phenophases.

To address our objectives, we pooled data across time and space by species to evaluate the relative consistency in timing for each phenophase for univariate comparisons. Spread in the distributions for timing of leaf, flower, and fruit for individual species was intended to inform two related interpretations. First, shape of the distributions depicts the level of confidence concerning the timing of a species' phenological transition. Second, histogram shapes represent species' responsiveness to inter-annual variability in environmental conditions such as extremes in air temperature and available soil moisture. Species with tall peaks or narrow inter-quartile ranges are those that undergo phenological stages with high consistency and are seemingly less responsive to varying environmental conditions spanning 1993–2015. In contrast, for multivariate analyses, we retained site specificity with species observations.

METHODS

Study site

The study was conducted at 15 sites on the USDA Agricultural Research Service Jornada Experimental Range and adjacent New Mexico State University Chihuahuan Desert Rangeland

Research Center that together constitute the Jornada Basin Long-Term Ecological Research (JRN LTER). The JRN occurs in the northern Chihuahuan Desert near Las Cruces, New Mexico, USA (central coordinates: 32.603° N, 106.776° W; Fig. 1), between the Rio Grande corridor to the west and the San Andres Mountains to the east within the southern Jornada del Muerto Basin (Southern Desertic Basins, Plains, and Mountains Major Land Resource Area; USDA-NRCS 2010). Soils at study sites range from clayey to sandy with variability in soil depth, gravel content, and subsurface carbonate accumulations (Duniway et al. 2018). In addition to local physical soil properties, landscape position and geomorphology also influence the distribution of moisture at a given location. Topographic wetness indices derived from digital elevation models quantify potential overland flow influences on soil moisture and provide an integrative means by which to contextualize landscapes in water-limited ecosystems as a function of topography. We used topographic indices to represent static environmental properties that varied spatially among sites. The JRN study site is characterized by a wide range of both PAW and topographic complexity and wetness (Fig. 1). Livestock grazing has declined from peaks in the late 1800s and 1910s (Fredrickson et al. 1998); current grazing intensities are maintained at low levels throughout the JRN (i.e., approximately 20 acres per animal unit month; Havstad et al. 2006).

The 15 sites were established in 1988 by the JRN LTER Program as part of a co-located long-term study on controls on patterns in aboveground plant primary production (Huenneke et al. 2002, Peters et al. 2012). The sites represent the range in variability in species composition, vegetation cover, soils, and landscape position for dominant plant communities in the Jornada del Muerto Basin (Fig. 1). Three sites were located within each of five ecological landscape types distinguished by the dominant plant species and landform (defined as the expression of soil parent material and landscape position): *Larrea tridentata* alluvial fan piedmont, *Flourensia cernua* alluvial flats, *Prosopis glandulosa* dune systems, *Bouteloua eriopoda* upland grasslands, and grass-dominated dry lakes (*Pleuraphis mutica*) or playas (*Panicum obtusum*; Huenneke et al. 2002). Variation in environmental conditions among
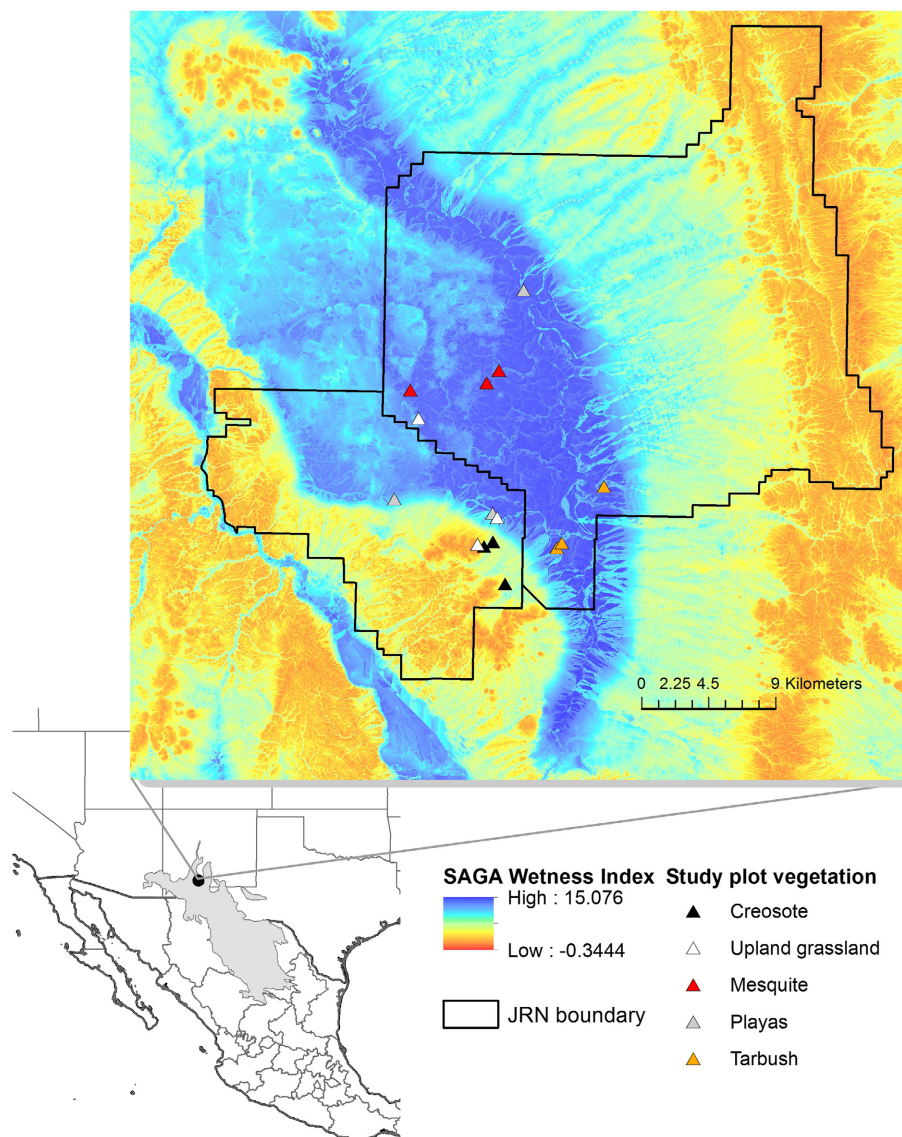
Fig. 1. Jornada Basin Long-Term Ecological Research site (black polygon) in southern New Mexico on a SAGA topographic wetness index image. High values denote water run-on areas. Monthly phenology observations are made at 15 long-term study sites since July 1992.

sites is reflected by ranges of key variables, with peak fall biomass ranging from 65 to 257 g/m^2 between 1989 and 2014, percent bare ground (i.e., unvegetated surface) from 2% to 59%, percent surface gravel from 0% to 55%, and PAW in the upper 50 cm of the soil profile from 1.7 to 9.4 cm (Appendix S1: Table S1). Topographic complexity and landscape-scale water distribution characterized by the SAGA wetness index (Boehner et al. 2002) using the SAGA Geographical User Interface version 2.1.1 (Conrad et al. 2015) ranged from 3.1 to 14.5 (Appendix S1: Table S1), where high values reflect areas of run-on and low values represent areas on the landscape typified by overland water flow.

Climate context

Long-term (80 yr) average annual rainfall (reported by water year from 1 October to 30

September) was 240.6 mm (Fig. 2). Approximately 56% of annual rainfall (135 mm) occurs from July to September from moisture originating in the gulfs of Mexico and California (hereafter "monsoon"). Mean maximum monthly temperatures over the same time period ranged from 13.5°C in January to 35.0°C in July (Wainwright 2006). The prominent period of drought from 2000 to 2003 related to ENSO variability at the JRN represents the broader pattern of drought during this period throughout much of the western United States (Cook et al. 2004). A sequence of record-breaking monsoon rainfall years in 2006 and 2008 that followed the 2003 drought resulted in an increase in perennial grass cover at many locations on the JRN (Peters et al. 2012, 2014).

Focal species

The ongoing JRN LTER plant phenology study began in July 1992; we report data through 2015. Initial study objectives were focused on longevity of seed and/or fruit production while encompassing other stages of the plant life cycle. Of the perennial species that have been monitored since July 1992, not all species are present at all sites. For this reason, the number of sites where each species was monitored ranges from one to seven (Table 1). We limited our analysis to those species for which we had eleven or more years of data. The remaining 16 species were ten warm season C_4 grasses and six shrub and sub-shrub species following the C_3 photosynthetic pathway. Of the C_3 shrub species, one is an evergreen

Fig. 2. Long-term average monthly precipitation (dark blue line) and temperature (dashed black line) for the Jornada Experimental Range weather station (#294426) from 1914 to 2014.

shrub (*L. tridentata*) and the remaining five species are deciduous (see Table 1 for details).

Long-term phenology protocols

Phenological status observations.—Phenology observations are made monthly for 16 focal species. Monthly observations consist of counts of individuals in one of five phenophases: (1) dormant, the production of (2) new leaves (i.e., initial growth prior to production of reproductive structures), (3) flower buds, (4) open flowers, or (5) fruit (or caryopses in the case of grasses). Individuals were counted based on the most advanced phenophase exhibited. Counts by phenophase are adapted from the density and line transect methods described in Herrick et al. (2005) within two 1 m × 75 m belt transects. Individual plants are assigned to the single, most advanced phenophase for a given survey.

Phenophase definitions are consistent across perennial growth forms (i.e., C_4 grasses and C_3 shrubs and sub-shrubs). The non-reproductive phenophase (herein used to determine first leaf) represents the production of new plant material; this phenophase encompasses the emergence of green basal shoots or greening of existing shoots in grasses and the production of leaf buds and/or unfolded leaves for shrubs. Flower budding corresponds to the production of flower buds prior to opening. For grasses, this coincides with emergence of the flower stalk or inflorescence, while in shrub species it corresponds to flower buds. Flowering is defined by open flowers (or florets in the case of grasses) wherein the reproductive structures of anthers and stigma are exposed and are visible; this distinction is common to grass and shrub species. Fruiting includes both production of seeds for shrubs and grains and production of caryopses for grasses; there is no distinction between developing and mature fruit. Production and retention of fruit takes precedence over onset of dormancy in this protocol, meaning that if fruit are present, this status, rather than dormancy, is reported in this method that allows for reporting only a single state. In this way, the protocol emphasizes reproductive phenology. Similarly, plants retaining fruit are counted as fruiting only until new leaves are produced, marking the transition to non-reproductive status the following growing season. Dormant denotes the period when plants
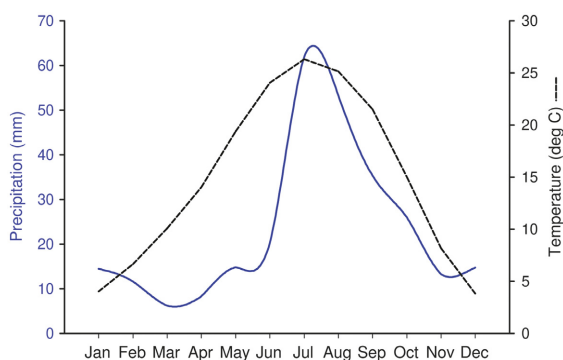
Table 1. Sixteen plant species included in this study.

Species	Species code	USDA code	Growth form	Photosynthetic pathway	No. sites
Bouteloua eriopoda	BOER	BOER4	Grass	C_4	3
Dasyochloa pulchella	DAPU	DAPU7	Grass	C_4	4
Eragrostis lehmanniana	ERLE	ERLE	Grass	C_4	1
Muhlenbergia arenacea	MUAR	MUAR	Grass	C_4	4
Muhlenbergia porteri	MUPO	MUPO2	Grass	C_4	7
Panicum obtusum	PAOB	PAOB	Grass	C_4	2
Pleuraphis mutica	PLMU	PLMU3	Grass	C_4	4
Scleropogon brevifolius	SCBR	SCBR2	Grass	C_4	4
Sporobolus airoides	SPAI	SPAI	Grass	C_4	2
Sporobolus flexuosus	SPFL	SPFL2	Grass	C_4	2
Flourensia cernua	FLCE	FLCE	Shrub	C_3	3
Gutierrezia sarothrae	GUSA	GUSA2	Sub-shrub	C_3	5
Larrea tridentata	LATR	LATR2	Shrub	C_3	3
Lycium berlandieri	LYBE	LYBE	Shrub	C_3	2
Prosopis glandulosa	PRGL	PRGL2	Shrub	C_3	4
Zinnia acerosa	ZIAC	ZIAC	Sub-shrub	C_3	2

Notes: Species names were taken from the Jornada Basin Long-Term Ecological Research website at https://jornada.nmsu.edu/lter/dataspecies/lter-plants. Grass nomenclature follows Allred (1983), and nomenclature for all other species follows Correll and Johnston (1970).

are not photosynthetically active. Dormancy is more readily denoted in deciduous shrubs as leaf drop, and in grasses as standing dry yellow leaves with no green growth. No dormancy phase is noted for the evergreen C_3 shrub *L. tridentata*.

Plant abundance by phenophase.—Among the 16 species monitored in this study, abundance within and among study sites and years can be highly variable, requiring use of two census methods for transect counts. On each monthly field visit, counts of individual plants in the most advanced of the five phenophases were made along the two 75-m transects described above. Changes in census method (belt vs. line transect) over the 23-yr record occurred for grasses due to large changes in abundance and preclude quantitative treatment of the abundance data. Rather, we use the counts by phenophase to derive phenometrics denoting the timing of first leaf, first bud or flower, and first fruit.

Deriving species-level phenological patterns

Phenology metrics were derived from monthly counts. To evaluate variability in the phenology of common plant species, we focused on three metrics: timing (i.e., month) of (1) initial growth or first leaf, (2) first flower bud or open flower (hereafter noted as "first flower"), and (3) first fruit. We defined first leaf, first flower, and first fruit as transitions that occur once a year for each species–site combination.

We implemented a sequential development criterion by establishing that month of first fruit could not precede month of first leaf or flower. Month of first leaf, first flower, and first fruit was tabulated for each species–site–year combination as the month in which (1) phenophase counts were greater than zero and (2) no missing observations occurred in the preceding month(s) of the calendar year. Two exceptions to the above rules were made for the evergreen shrub *L. tridentata*: (1) Month of first leaf was not noted and (2) only the first flower event was tabulated even though *L. tridentata* can flower more than once a year, especially in highly variable systems (Crimmins et al. 2014, Mazer et al. 2015).

Deriving the phenological metrics was complicated in two circumstances. The first case was missing observations that arose either when study sites were not accessible or when observers failed to observe all species at a given site. The second circumstance applied to species with ephemeral and/or subtle phenophase changes that were difficult to detect or poorly captured with monthly observations. If monthly counts for a given phenophase were zero in all months, that site–species–year record was classified as not observed. Years in which the month or months preceding the increase from zero for a given phenophase were missing, the phenophase observations were denoted as indiscernible and no data

in the hierarchical cluster analysis (see "Site- and species-level phenological patterns across time").

Species phenological patterns across space

To examine consistency by species in the timing of phenophase onsets using frequency distributions of month of first leaf, flower, and fruit, we pooled data across sites (see species–site combinations in Table 1). Percentages reported represent discernible observations (i.e., excluding indiscernible or missing data). Modes for distributions were identified as the local maxima within a three-month window. Distributions were then evaluated using a series of pairwise comparisons using the Wilcoxon Z test.

Site- and species-level phenological patterns across time

To determine whether phenological guilds emerged via inter-annual coherence in the timing of first leaf, flower, and fruit production, we used agglomerative hierarchical cluster analysis using the vegan package (Oksanen et al. 2018) in R version 3.2.5. We decided a priori to interpret cluster analysis results if the species–site combinations resolved into clusters with a reasonable degree of evenness regarding membership of species–site combinations in each cluster (sensu Clarke and Warwick 2001).

We performed cluster analyses separately for leaf, flower, and fruit. In each data matrix, site–species combinations were row headings, years were column headings (1993–2015), and values in the columns were months of the year (ordinal values). We performed hierarchical, agglomerative clustering with Ward's linkage method based on a Euclidian distance matrix for each phenophase (Ward 1963, Kaufman and Rousseeuw 2009). Hierarchical cluster analysis with Euclidean distance and Ward's method has been used in studies seeking to identify phenological similarities among sites across years, with ordinal data (Golluscio et al. 2005) and categorical data (Pfister et al. 1996) as variables. To our knowledge, this is the first phenology study that clustered species–site combinations in terms of their variation among years, with ordinal data representing (months) as values in the year variables.

We apply the guild concept (Root 1967, Gurevitch et al. 2006) to phenology and, in this case, maintain site specificity in the data matrices. Root

(1967) defined guilds as "a group of species that exploit the same class of environmental resources in a similar way." We expand this definition of a guild to represent phenological responses (i.e., timing) to environmental conditions which may or may not represent overlap in niche requirements. We define a phenological guild as a cluster of three or more species with fidelity in the timing of a given phenophase over time. If a group contains observations for only one or two species, it is a cluster rather than a guild. All guilds are clusters, but not all clusters are guilds. A guild can include species at the same or different site locations. Ultimately, the number of clusters selected for interpretation was based on a combination of results from Mantel tests coupled with expert knowledge of the system.

We used Mantel tests to objectively prune the cluster dendrograms to the optimum number of clusters—that is, clusters with maximum within-cluster similarity and between-cluster dissimilarity. The Mantel technique iteratively compares the original distance matrix to multiple binary matrices representing cluster assignments computed from the dendrogram and then identifies the dendrogram level (i.e., the number of clusters) with the greatest matrix correlation (r) between the binary matrix and original matrix (Borcard et al. 2011). We generated bubble plots for each cluster, which depict the number of species–site cluster members undergoing a particular phenophase transition in each month.

Results

Patterns in the timing of first leaf, first flower, and first fruit across space

All 16 species generally initiated growth prior to the onset of monsoon rains (c. 1 July; Fig. 3). Data were pooled across sites for univariate analyses. Some species exhibited remarkable consistency in the timing from year to year and across sites for initial growth (e.g., *Gutierrezia sarothrae* and *Flourensia cernua* in January and *Prosopis glandulosa* in April), whereas others were more variable (e.g., *Lycium berlandieri*, *Zinnia acerosa*, and *Muhlenbergia arenacea*). For example, a large proportion of first leaf observations for *P. glandulosa* (>60%) occurred in April; in contrast, first leaf for *Dasyochloa pulchella* occurred over a span of eight months (Fig. 3). Distributions for month
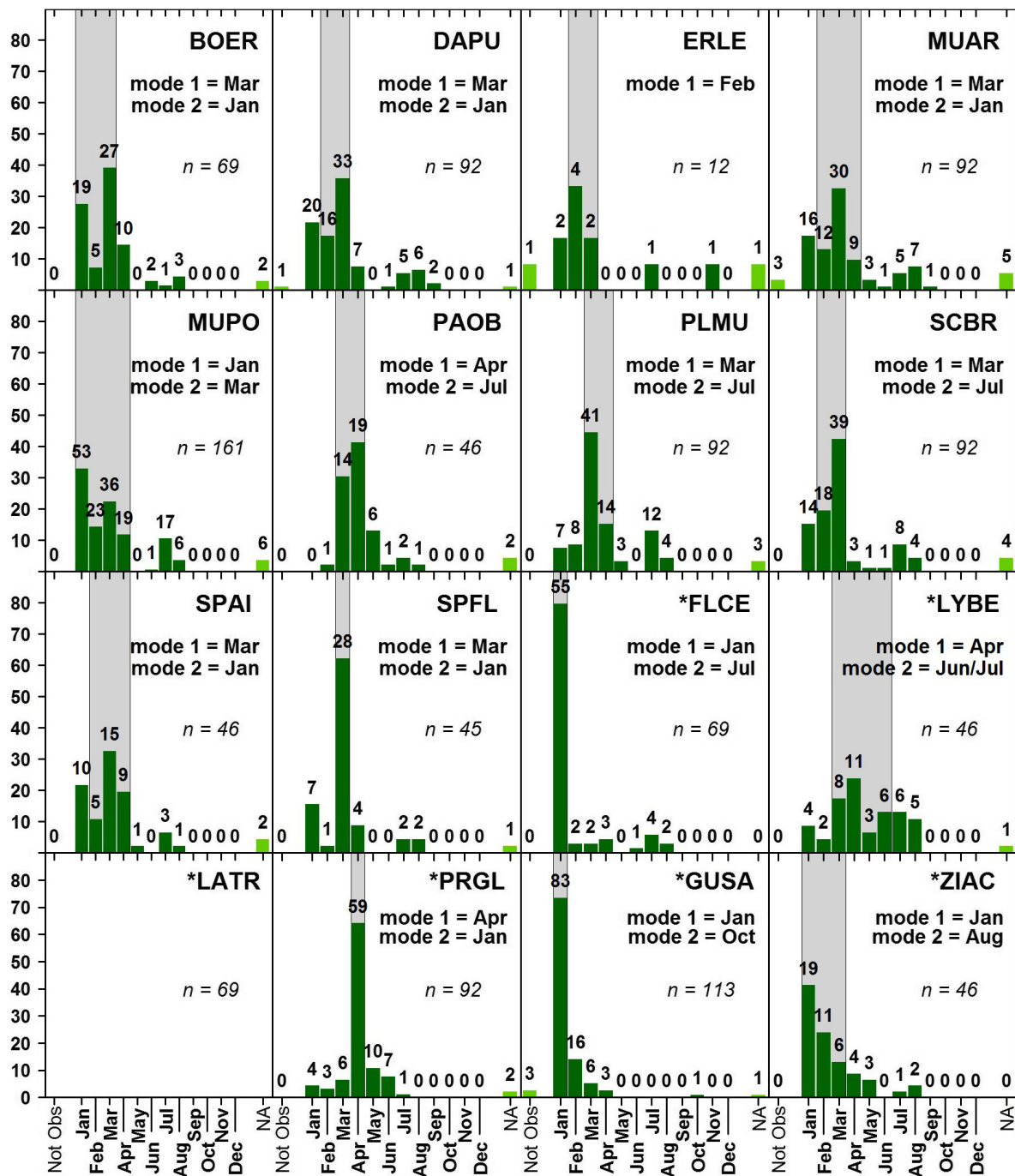
Fig. 3. Frequency distributions for the appearance of first leaves for 15 species at Jornada Basin between 1993 and 2015; four-letter species codes are defined in Table 1. LATR is an evergreen shrub; the first leaf metric does not apply. Numbers above bars represent the number of observations across all site–species–year combinations. Gray shading denotes the inter-quartile range in which 50% of observations occur. Values of 0 indicated initial growth was not observed in the 12 months (Not Obs), whereas the inability to identify initial growth due to missing observations is denoted as NA. Percentages (*y*-axes) are based on the number of all site–year combinations excluding Not Obs and NA records.

of first flower were roughly centered (i.e., extent of inter-quartile range) on July and August for most C_4 grasses and occurred in June for C_3 shrubs *P. glandulosa* and *Larrea tridentata* (Fig. 4). Distributions for month of first fruit were wider (i.e., least consistent of the three phenophases) with higher consistency in timing of first fruit for *P. glandulosa* and *F. cernua* (Fig. 5).

Wilcoxon *Z* tests broadly revealed significant differences in the distributions for timing of first leaf, flower, and fruit. Of the 45 pairwise comparisons among C_4 grasses, only eight (17.8%) and seven (15.5%) pairwise comparisons indicated the distributions for timing of first leaf (Table 2) and flower (Table 3) were significantly different, respectively. For first fruit, only three C_4 pairwise comparisons (6.7%) were significantly different (Table 4). The timing of first leaf for *Panicum obtusum* differed from most other C_4 grasses (7 of 8 significant differences; Table 2) initiating growth later with 50% of observations occurring in April and May (Fig. 3). All C_4 grasses (except *Eragrostis lehmanniana* monitored at one site) exhibited bimodal distributions in the timing of first leaf, such that in most years, first leaf occurred in March, but in a small number of years, these species leafed out in summer months (primarily June, July, August, and September; Fig. 3). Timing of first flower for *Pleuraphis mutica* differed most commonly from other C_4 grasses (six of seven significant differences; Table 3) with a unimodal distribution centered on August vs. the more common bimodal distributions for other grasses (Fig. 4). Distributions for the timing of first fruit were also largely congruent for C_4 grasses. Timing of first fruit for *P. mutica* was significantly different from distributions for *M. arenacea, Muhlenbergia porteri*, and *Sporobolus flexuosus* (Table 4) with a larger inter-quartile range (Fig. 5).

In contrast to C_4 grasses, distributions for phenology for C_3 shrubs more frequently differed from each other. At the species level, distributions for all phenophases for C_3 shrubs *G. sarothrae, F. cernua, P. glandulosa,* and *L. tridentata* differed significantly from most other species (Tables 2–4). *Prosopis glandulosa* consistently produced first fruit in June, while other C_3 species (i.e., *L. berlandieri* and *Z. acerosa*) exhibited remarkable interannual variability in the timing of first fruit, with first fruit appearing across seven to ten months of the year (Fig. 5). In eight of the ten pairwise

comparisons among C_3 shrubs for timing of first leaf (excluding *L. tridentata*), the distributions for timing of first leaf were significantly different (Table 2). Of the 15 pairwise comparisons for timing of first flower and fruit for C_3 shrubs, there were 11 significantly different species-pair combinations (Tables 4, 5). Patterns in timing emerged. For first leaf, *F. cernua* and *G. sarothrae* exhibited a strong and consistent pattern in January while *P. glandulosa* and *L. berlandieri* most commonly leafed out in April (Fig. 3). For first flower, *G. sarothrae* and *L. berlandieri* shared first and second modes in the distributions in July and September (Fig. 4). As in case of C_4 grasses, distributions of the timing for first fruit for C_3 shrubs demonstrated fewer pairwise differences than did first leaf and flower; however, 33% of the pairwise comparisons for C_3 shrubs first fruit were significantly different. For reproductive phenophases, C_3 shrubs tended to have a single mode (or higher peaks) while C_4 grass distributions were more evenly spread across months (Figs. 4, 5). Early and late instances of first leaf, first flower, and first fruit occurred in approximately equal proportions across study sites that vary in topoedaphic properties, namely PAW and topographic wetness (Appendix S1: Table S1).

Not all phenophases were observed between 1993 and 2015. Cases in which field observations were made every month, but phenophases were not observed, occurred at some point in the time series for all species but *L. tridentata*. This inconsistency occurred more commonly for flower (Fig. 4) followed by fruit (Fig. 5) and least commonly for leaf (Fig. 3). Species–site–year cases with no record of flowering or fruit production occurred most commonly for the C_3 shrub *L. berlandieri* (Fig. 4). The fruit phenophase is a more reliable metric of reproductive effort since fruits are typically retained longer than flowers. *Lycium berlandieri* incurred the largest number of cases with no fruit (21 site–year cases; Fig. 5) followed by C_4 grasses *M. porteri* and *M. arenacea* with 17 and 12 cases, respectively, C_3 shrubs *G. sarothrae* and *F. cernua* with 13 cases each and *P. glandulosa* with 10 cases, and the C_4 grass *S. flexuosus* with 10 cases over the 23-yr period (Fig. 5).

Cluster analysis

The cluster analysis yielded a reasonable degree of evenness of species–site membership in the
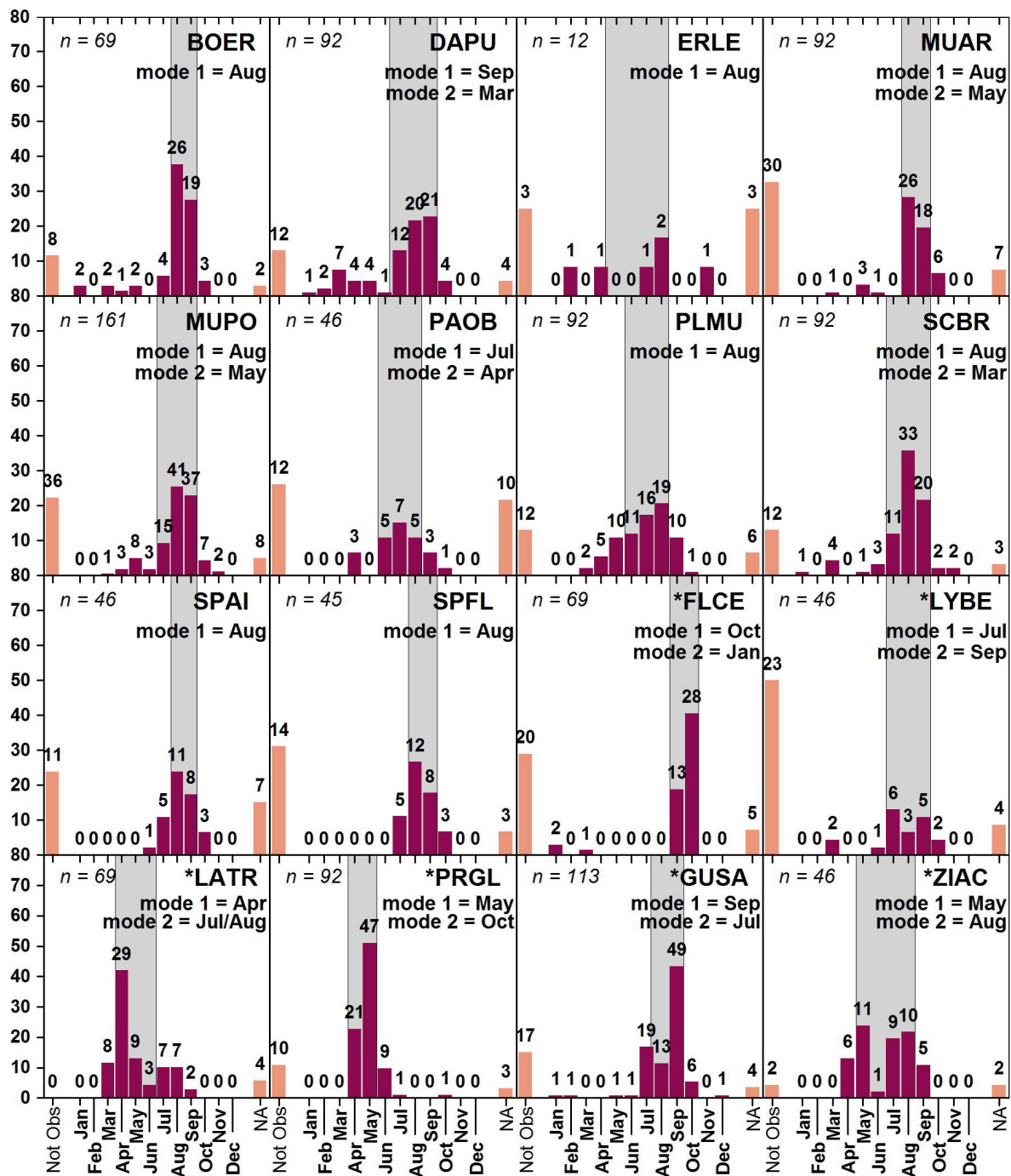
Fig. 4. Frequency distributions for the appearance of first flower or flower bud for 16 species at Jornada Basin between 1993 and 2015; four-letter species codes are defined in Table 1. Numbers above bars represent the number of observations across all site–species–year combinations. Gray shading denotes the inter-quartile range in which 50% of observations occur. Values of 0 indicated flowers were not observed in the 12 months (Not Obs), whereas the inability to identify flowering due to missing observations is denoted as NA. Percentages (y-axes) are based on the number of all site–year combinations excluding Not Obs and NA records.
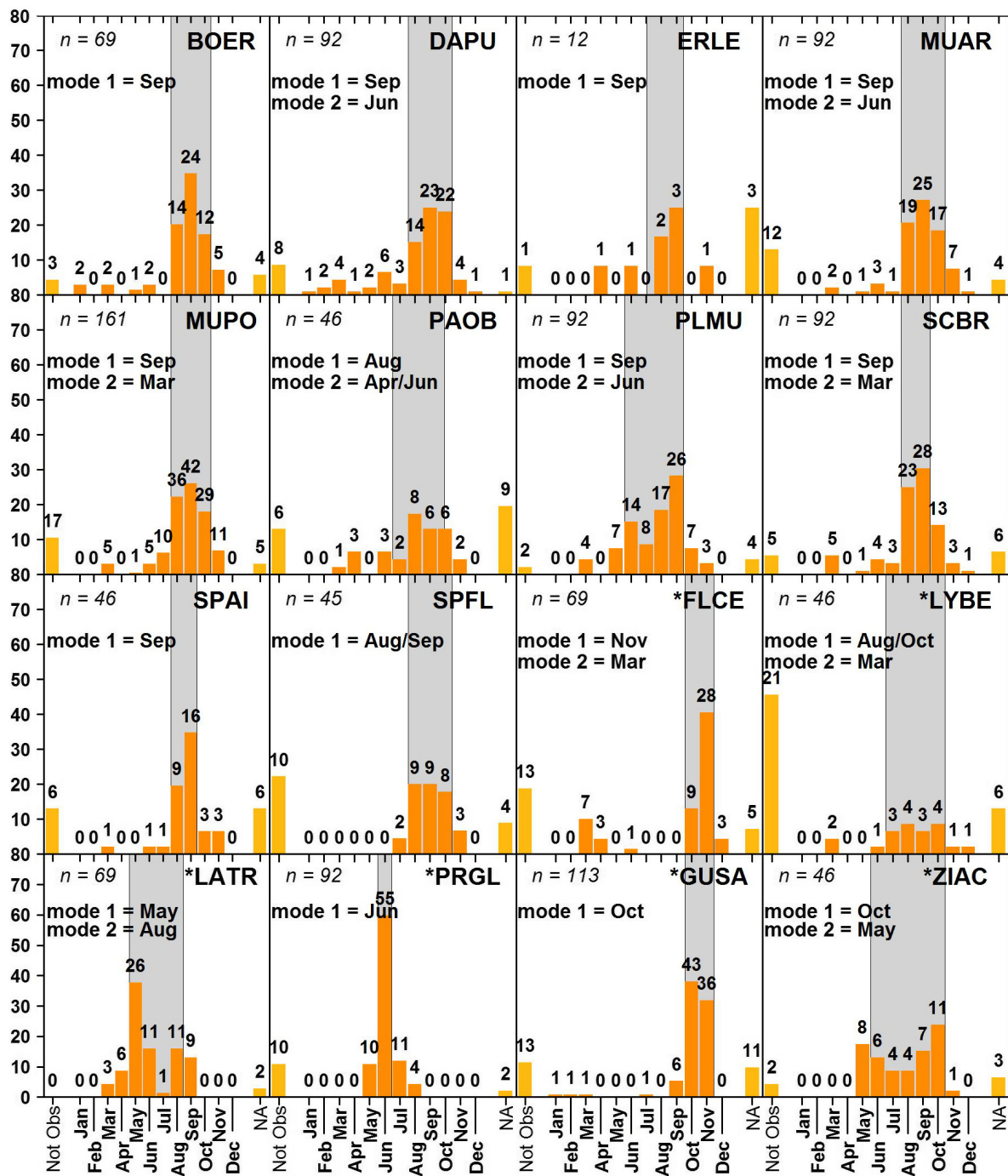
Fig. 5. Frequency distributions for the appearance of first fruit for 16 species at Jornada Basin between 1993 and 2015; four-letter species codes are defined in Table 1. Numbers above bars represent the number of observations across all site–species–year combinations. Gray shading denotes the inter-quartile range in which 50% of observations occur. Values of 0 indicated fruits were not observed in the 12 months (Not Obs), whereas the inability to identify fruiting due to missing observations is denoted as NA. Percentages (y-axes) are based on the number of all site–year combinations excluding Not Obs and NA records.

Table 2. Contingency table with *P*-values for pairwise comparisons using the Wilcoxon *Z* test for distributions representing month of first leaf for 10 perennial C_4 grass plant species on the Jornada Basin; significant differences ($\alpha < 0.05$) are noted in bold and with an asterisk.

Species	C_4 grasses								
	DAPU	ERLE	MUAR	MUPO	PAOB	PLMU	SCBR	SPAI	SPFL
BOER	1.00	0.999	0.997	1.000	**<0.001***	0.173	1.000	1.000	1.000
DAPU		0.994	1.000	0.998	**<0.001***	0.177	1.000	1.000	0.999
ERLE			0.943	1.000	0.075	0.339	0.953	0.991	0.803
MUAR				0.731	**0.039***	0.934	1.000	1.000	1.000
MUPO					**<0.001***	**0.007***	0.984	0.998	0.943
PAOB						0.460	**<0.001***	**0.023***	**0.002***
PLMU							0.152	0.871	0.906
SCBR								1.000	0.999
SPAI									1.000
SPFL									
FLCE									
GUSA									
LYBE									
PRGL									

Note: Species codes are defined in Table 1.

(Table 2. Continued.) Contingency table with *P*-values for pairwise comparisons using the Wilcoxon *Z* test for distributions representing month of first leaf for 15 perennial plant species on the Jornada Basin; first leaf does not apply to the evergreen shrub (*Larrea tridentata*).

Species	C_3 shrubs					
	FLCE	GUSA	LATR	LYBE	PRGL	ZIAC
BOER	**<0.001***	**<0.001***		**<0.001***	**<0.001***	0.898
DAPU	**<0.001***	**<0.001***		**0.003***	**<0.001***	0.578
ERLE	0.229	0.103		0.285	**0.029***	1.000
MUAR	**<0.001***	**<0.001***		**0.042***	**<0.001***	0.172
MUPO	**<0.001***	**<0.001***		**<0.001***	**<0.001***	0.989
PAOB	**<0.001***	**<0.001***		0.986	0.999	**<0.001***
PLMU	**<0.001***	**<0.001***		0.258	**0.010***	**0.001***
SCBR	**<0.001***	**<0.001***		**0.001***	**<0.001***	0.287
SPAI	**<0.001***	**<0.001***		**0.020***	**<0.001***	0.698
SPFL	**<0.001***	**<0.001***		**0.009***	**<0.001***	0.249
FLCE		1.000		**<0.001***	**<0.001***	**0.032***
GUSA				**<0.001***	**<0.001***	**0.001***
LYBE					0.990	**<0.001***
PRGL						**<0.001***

Notes: Significant differences ($\alpha < 0.05$) are noted in bold and with an asterisk. Species codes are defined in Table 1.

clusters for timing of first leaf and first fruit, suggesting the presence of phenological guilds. We used Mantel tests and knowledge about the system to prune the cluster dendrograms to the optimum number of clusters (Fig. 6). For leaf, the levels of the dendrogram with the largest Mantel *r* values were those corresponding to two, three, and six clusters (*r* = 0.588, 0.589, and 0.518, respectively).

As two and three clusters resulted in the loss of critical information about the system, we cut the leaf dendrogram at six clusters (Fig. 6A). For fruit, the levels of the dendrogram with the largest *r* values corresponded to eight, seven, and six clusters (*r* = 0.452, 0.444, and 0.430, respectively). Both eight and seven cluster dendrograms resulted in models in which there was duplicative

Table 3. Contingency table with *P*-values for pairwise comparisons using the Wilcoxon *Z* test for distributions representing month of first flower or flower bud for 10 perennial C_4 grass plant species on the Jornada Basin; significant differences ($\alpha < 0.05$) are noted in bold and with an asterisk.

Species	C_4 grasses								
	DAPU	ERLE	MUAR	MUPO	PAOB	PLMU	SCBR	SPAI	SPFL
BOER	0.944	0.996	0.996	1.000	0.207	**0.003***	1.000	1.000	1.000
DAPU		1.000	0.213	0.747	0.998	0.857	0.997	0.901	0.818
ERLE			0.931	0.995	1.000	1.000	0.999	0.992	0.984
MUAR				0.990	**0.016***	**<0.001***	0.739	1.000	1.000
MUPO					0.147	**<0.001***	1.000	1.000	1.000
PAOB						1.000	0.339	0.146	0.076
PLMU							**0.006***	**0.007***	**0.003***
SCBR								1.000	0.998
SPAI									1.000

Note: Species codes are defined in Table 1.

(Table 3. Continued.) Contingency table with *P*-values for pairwise comparisons using the Wilcoxon *Z* test for distributions representing month of first flower or flower bud for 15 perennial plant species on the Jornada Basin; significant differences ($\alpha < 0.05$) are noted in bold and with an asterisk.

Species	C_3 shrubs					
	FLCE	GUSA	LATR	LYBE	PRGL	ZIAC
BOER	**<0.001***	0.880	**<0.001***	1.000	**<0.001***	**0.003***
DAPU	**<0.001***	**0.027***	**<0.001***	1.000	**<0.001***	0.687
ERLE	0.502	0.937	0.992	1.000	0.962	1.000
MUAR	**<0.001***	1.000	**<0.001***	0.953	**<0.001***	**<0.001***
MUPO	**<0.001***	0.723	**<0.001***	1.000	**<0.001***	**<0.001***
PAOB	**<0.001***	**0.004***	**0.002***	0.995	**<0.001***	1.000
PLMU	**<0.001***	**<0.001***	**<0.001***	0.919	**<0.001***	1.000
SCBR	**<0.001***	0.296	**<0.001***	1.000	**<0.001***	**0.005***
SPAI	**<0.001***	1.000	**<0.001***	0.999	**<0.001***	**0.004***
SPFL	**<0.001***	1.000	**<0.001***	0.994	**<0.001***	**0.002***
FLCE		**<0.001***	**<0.001***	**0.001***	**<0.001***	**<0.001***
GUSA			**<0.001***	0.904	**<0.001***	**<0.001***
LATR				**0.003***	0.948	**0.002***
LYBE					**<0.001***	0.780
PRGL						**<0.001***

Note: Species codes are defined in Table 1.

information, so we elected to cut the dendrogram at six clusters (Fig. 6B). As such, a six-cluster model optimally conveyed the similarity of species–site combinations with respect to timing (January–December) of both first leaf and first fruit across the 23-yr study period. The levels of the flower dendrogram identified as optimal corresponded with 19, 20, and 18 clusters ($r = 0.469$, 0.468, and 0.467, respectively). We attribute the larger number of clusters to the zero-inflation in the flower matrix, due to missing records that precluded interpretable clusters. Clusters for timing of

first flower were indiscernible; we did not report those results.

Variability in phenology across space and time—coherent clusters

Guilds comprise three or more species, while clusters consist of only one or two species. In both cases, species can occur at the same or different sites. Leaf clusters ranged in size from 3 to 21 species–site observations (Fig. 6A). Of the six leaf clusters, one contained only two members of one C_4 grass genus (hereafter "Bush Muhly leaf

Table 4. Contingency table with *P*-values for pairwise comparisons using the Wilcoxon *Z* test for distributions representing month of first fruit for 10 perennial C_4 grass plant species on the Jornada Basin; significant differences ($\alpha < 0.05$) are noted in bold and with an asterisk.

Species	C_4 grasses								
	DAPU	ERLE	MUAR	MUPO	PAOB	PLMU	SCBR	SPAI	SPFL
BOER	1.000	0.998	1.000	1.000	0.983	0.055	0.997	1.000	1.000
DAPU		1.000	0.999	1.000	1.000	0.302	1.000	1.000	1.000
ERLE			0.987	1.000	1.000	1.000	1.000	0.999	0.986
MUAR				0.999	0.834	**0.003***	0.894	1.000	1.000
MUPO					0.987	**0.010***	1.000	1.000	1.000
PAOB						1.000	1.000	0.997	0.884
PLMU							0.412	0.292	**0.039***
SCBR								1.000	0.969
SPAI									1.000

Note: Species codes are defined in Table 1.

(Table 4. Continued.) Contingency table with *P*-values for pairwise comparisons using the Wilcoxon *Z* test for distributions representing month of first fruit for 15 perennial plant species on the Jornada Basin; significant differences ($\alpha < 0.05$) are noted in bold and with an asterisk.

Species	C_3 shrubs					
	FLCE	GUSA	LATR	LYBE	PRGL	ZIAC
BOER	**0.001***	**<0.001***	**<0.001***	1.000	**<0.001***	0.911
DAPU	**<0.001***	**<0.001***	**<0.001***	1.000	**<0.001***	0.994
ERLE	0.520	**0.011***	0.401	1.000	**0.024***	1.000
MUAR	**0.002***	**<0.001***	**<0.001***	0.998	**<0.001***	0.492
MUPO	**<0.001***	**<0.001***	**<0.001***	1.000	**<0.001***	0.756
PAOB	**0.010***	**<0.001***	**0.004***	1.000	**<0.001***	1.000
PLMU	**<0.001***	**<0.001***	**<0.001***	0.999	**<0.001***	1.000
SCBR	**<0.001***	**<0.001***	**<0.001***	1.000	**<0.001***	0.998
SPAI	**0.010***	**<0.001***	**<0.001***	1.000	**<0.001***	0.976
SPFL	0.053*	**<0.001***	**<0.001***	0.997	**<0.001***	0.579
FLCE		0.991	**<0.001***	0.209	**<0.001***	**0.002***
GUSA			**<0.001***	**0.002***	**<0.001***	**<0.001***
LATR				**0.022***	0.819	**0.001***
LYBE					**<0.001***	1.000
PRGL						**0.001***

Note: Species codes are defined in Table 1.

cluster"), one contained a large group of C_4 grasses (hereafter "C_4 Grass Leaf Guild"), three clusters contained mostly C_3 shrub species (Mesquite, Snakeweed, and Tarbush leaf clusters), and one comprised a mix of two C_4 grasses and one C_3 shrub (hereafter "Playa Grass Leaf Guild").

In contrast to the tendency for many of the species to have all records of their occurrence appear in the same leaf cluster, three species are spread across several leaf clusters. *Muhlenbergia arenacea*, found at four sites in the study, appears in three clusters. Similarly, *P. mutica*, which is found at four sites, appears in two clusters, and *P. obtusum* observations from two sites occur in two clusters. Notably, two of the three species split across leaf clusters occur at playa sites (*P. mutica* and *P. obtusum*) where flood events play an important role in primary productivity (Peters et al. 2006).

The six fruit clusters ranged in size from 2 to 16 species–site observations (Fig. 6B): C_4 Grass Fruit Guild 1, C_4 Grass Fruit Guild 2, Tarbush–Dropseed (*Flourensia–Sporobolus*) Fruit Guild, Wolfberry (*L. berlandieri*) fruit cluster, Snakeweed
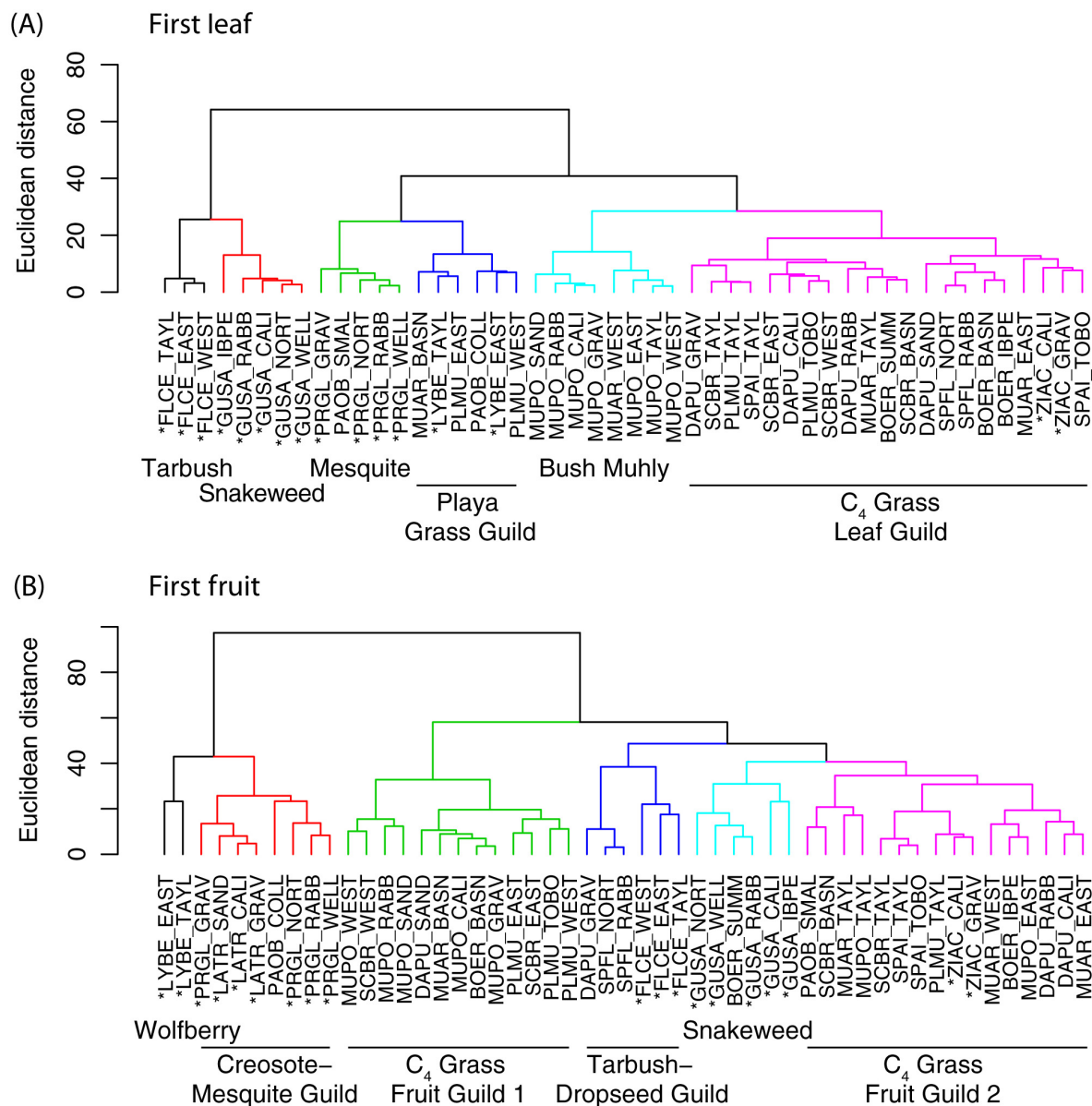
Fig. 6. Dendrograms generated using an agglomerative hierarchical cluster analysis for matrices including the month of first recorded leaf (A) and fruit (B) for 16 species occurring at one or more of 15 long-term study sites. Clusters for leaf and fruit are color-coded. Data span 1993–2015. Species with C_3 photosynthetic pathway are noted with an asterisk.

(*G. sarothrae*) fruit cluster, and the Creosote–Mesquite (*Larrea–Prosopis*) Fruit Guild.

High phenological consistency was observed both within and among species for first leaf and first fruit, regardless of site on which the species were situated (Figs. 6–8), as demonstrated in dendrograms and bubble plots. The leaf

phenology of *M. porteri* underscores this pattern: Across seven sites, *M. porteri* expressed initial growth with very high temporal consistency despite variation in site conditions (Figs. 6A, 7E). Similarly, timing of first fruit for *L. tridentata*, *G. sarothrae*, and *F. cernua* showed high phenological consistency (Fig. 8C, D). In contrast, some

species exhibited greater phenological variability, with the species split across clusters (e.g., *D. pulchella* and *P. obtusum* for timing of first fruit; Fig. 6B). Nearly all C_4 species showed very high within-year consistency across sites in the timing of first fruit (i.e., regardless of site or species they are fruiting with similar monthly patterns), whereas C_3 species resolved into species-specific groups (e.g., the Snakeweed and Wolfberry fruit clusters). Generally, the six clusters for timing of first fruit differed from those for first leaf in two ways: (1) Fruit clusters (Fig. 6B) exhibited greater multi-species membership than did leaf clusters (Fig. 6A), and (2) within-year variability in the timing of first fruit was higher than that for first leaf, reflected in the temporal spread (*y*-axis) apparent in the bubble graphs (Figs. 7, 8).

DISCUSSION

Patterns across phenophases and functional groups

Phenological studies in arid environments commonly focus on reproductive phenophases such as flowering (Seghieri et al. 2009, Crimmins et al. 2010, 2013*a*, Gremer et al. 2015, Munson and Long 2017). Few studies feature long-term patterns for multiple phenophases. Our focus in this study included one vegetative and two reproductive phenophase transitions. Analysis of the first leaf phenophase revealed the surprising pattern that all species—C_4 and C_3—initiated growth prior to monsoon rains in July. In addition, our evaluation of three phenophases over 23 yr revealed greater spread in the distributions for timing of first fruit relative to first leaf and first flower. This could be related to inter-annual variability in rainfall and soil moisture as demonstrated in a 12-yr study by Beatley (1974) in the Mojave Desert. Spread in the distributions for all phenophases for C_4 grasses was greater than that observed for C_3 shrubs.

The ability to anticipate the timing of phenological transition is important to a wide range of management applications. For example, phenological information can guide the selection of species to be used in grassland restoration to include species that initiate leafing, flowering, or fruiting over the course of the season (Buisson et al. 2017). Having confidence in when species will undergo transitions is also critical for managing migration of livestock herds to avoid periods of flowering or seed set for plant species of management concern (James et al. 2015), and to predict differential use of pastures by heritage and conventional cattle breeds that differ in their selection of forage resources (S. Spiegal et al., *unpublished manuscript*). Long-term datasets can yield new insights and help identify knowledge gaps that may pose challenges for predicting and management. In particular, species that demonstrate greater variability in the timing of flower and fruit production indicate a greater need to identify the environmental drivers of reproductive phenology for a given ecosystem.

Phenological consistency across sites and years

Pooling data across sites and years for the univariate analysis allowed us to evaluate the tendency of timing of phenophases and provided an understanding of the level of confidence in phenophase predictions and species responsiveness to extremes in temperature and water availability. For instance, *Prosopis glandulosa*—a deep-rooted C_3 shrub (>5 m; Gibbens and Lenz 2001)—exhibited consistent phenology at the JRN. The species' predictability indicates it can be anticipated with a reasonably high level of confidence which holds implications for management efforts to curtail proliferation of this species in desert grasslands. The month of leaf-out, flowering, and fruit production was consistent, despite great inter-annual and cross-site variation in environmental conditions between 1993 and 2015. Our findings coincide with 1978–1980 observations by Kemp (1983) who observed consistency in *P. glandulosa* timing of leaf-out (April), flower (April), and fruit production (May). Conversely, species exhibiting short, wide histograms such as *Dasyochloa pulchella* are seemingly more responsive to antecedent and concurrent conditions, and therefore require knowledge of drivers to accurately predict. *Dasyochloa pulchella* is considered a colonizing species that establishes in open areas and in so doing can reduce soil erosion that makes sites amenable for establishment of more desirable perennial grass species (Pezzani and Montana 2006).

We anticipated that shallow-rooted C_4 grasses would exhibit greater variability in timing of initial growth than C_3 shrub species with deeper root systems that provide access to deeper soil
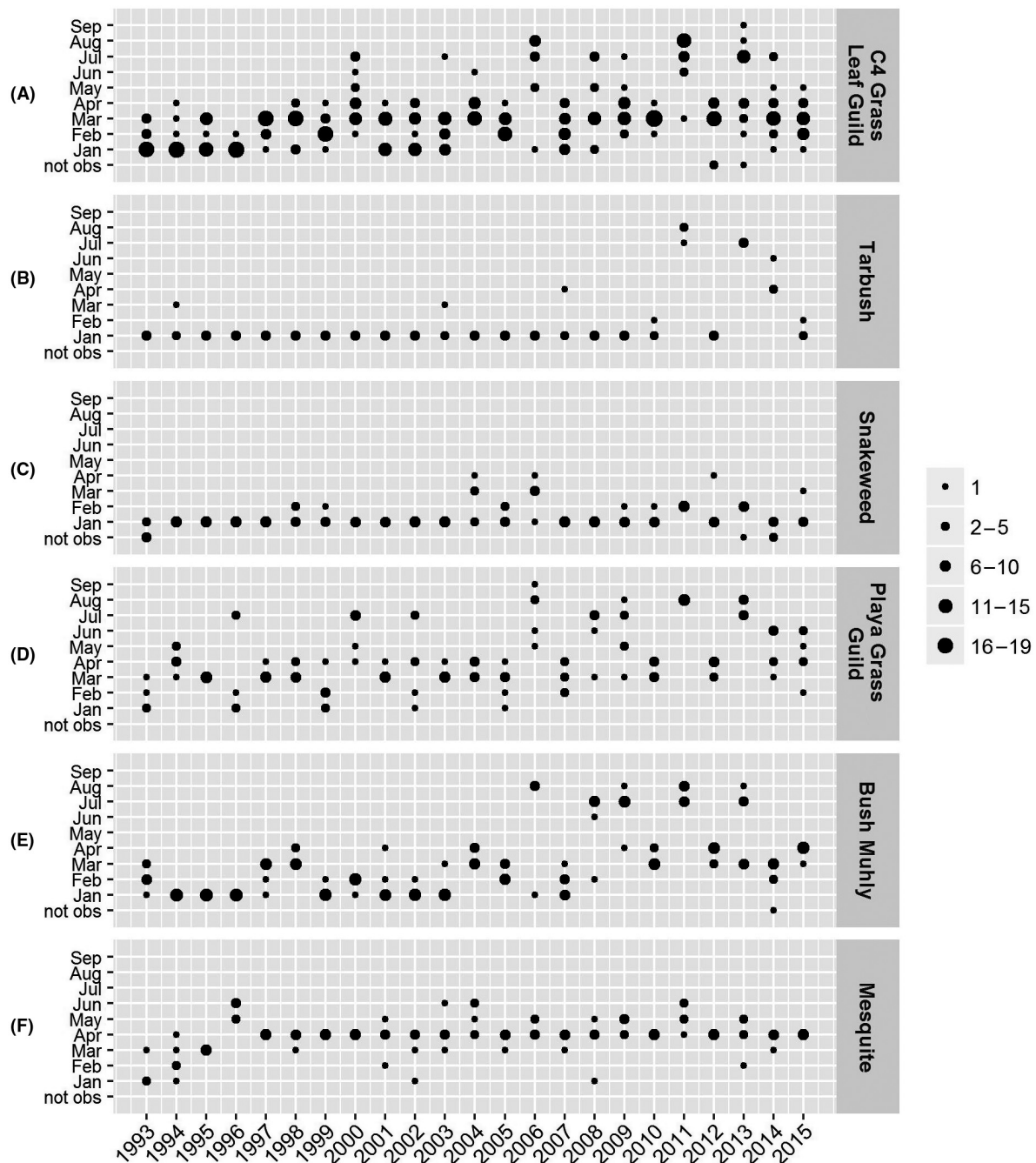
Fig. 7. Bubble plots representing patterns in timing of first leaf for six clusters (i.e., phenological guilds) over 23 yr. Bubbles reflect the count of count of species–site instances observed in first leaf in a particular month and year. (A) C4 Grass Leaf Guild cluster; (B) Tarbush cluster; (C) Snakeweed cluster; (D) Playa Grass Guild cluster; (E) Bush Muhly cluster; and (F) Mesquite cluster.
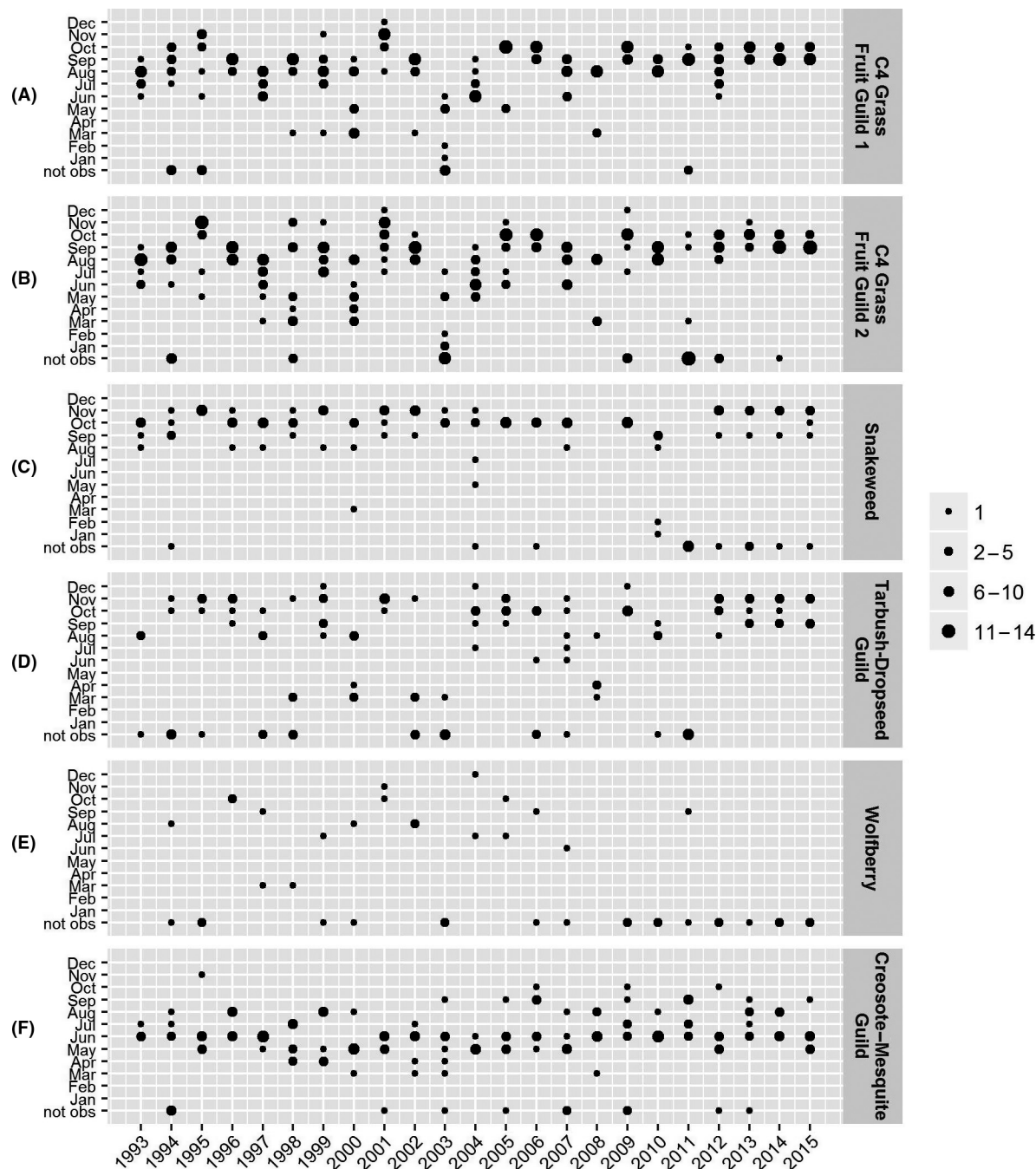
Fig. 8. Bubble plots representing patterns in timing of first fruit for six clusters (i.e., phenological guilds) over 23 yr. Bubbles reflect the count of species–site instances observed in fruit in a particular month and year. (A) C4 Grass Fruit Guild 1 cluster; (B) C4 Grass Fruit Guild 2 cluster; (C) Snakeweed cluster; (D) Tarbush–Dropseed Guild cluster; (E) Wolfberry cluster; and (F) Creosote–Mesquite Guild cluster.

moisture reserves. Results from the univariate analyses supported this prediction. In addition, we predicted that the timing of initial growth would be more variable than the timing of first flower or fruit. Qualitative assessments of histograms and extents of the inter-quartile range did not conclusively support this prediction; across all phenophases, the data exhibited considerable variation across species that were pooled across sites and years.

Coherency in timing of phenophases among years: identifying phenological guilds

The hierarchical cluster analysis and related dendrograms revealed patterns in phenology over time and led to the identification of groups of species–site instances that demonstrate inter-annual coherence in timing of leafing, flowering, or fruiting, over the 23-yr study period. In other words, the dendrograms highlight species which show consistent timing phenology across sites, regardless of year-to-year variation. This highlights a unique aspect of this study in that we maintained year-specific phenological events and our choice of clusters from the hierarchical cluster analysis was data-driven. The decision to analyze species–site instances was motivated by two factors: the range in soil and site conditions at the 15 sites and the unbalanced study design. In another study that used multivariate clustering techniques, Golluscio et al. (2005) conducted a 12-yr study of plant phenology in arid Patagonia to analyze associations between phenology patterns and life-form groups. Golluscio et al. (2005) collapsed phenological metrics across years in the input matrix, and the choice of clusters was influenced by the number of life-forms across the 25 species.

High phenological consistency within and among particular species across different site types (e.g., *Muhlenbergia porteri* for first leaf and *Larrea tridentata*, *Gutierrezia sarothrae*, and *Flourensia cernua* for first fruit) suggests that these species are adapted to variable site conditions or are invariant to them. In contrast, the timing of first fruit is split across clusters for phenologically variable species *D. pulchella* and *Panicum obtusum*, suggesting that phenology of these species may be more influenced by local site conditions.

Cluster membership for first fruit revealed clear patterns for reproductive phenology of C_3

and C_4 species. C_4 species exhibited very high within-year consistency across sites, and C_3 species resolved into species-specific groups. This suggests that within a single year, different C_3 species produce fruits at different times, which supports the theory of differential partitioning of resources coexistence in water-limited ecosystems (Noy-Meir 1973, Browning et al. 2012). Phenological consistency in exclusive cluster membership of C_4 grasses was also found by Golluscio et al. (2005) in their 12-yr study of phenology in the Patagonian steppe. Several distinct groups of species showed consistent within-year timing; this pattern also suggests temporal waves of flowering within this community, a pattern that has also been documented in the Sonoran Desert (Crimmins et al. 2013b).

When interpreted in tandem, the histograms and cluster analyses revealed unique patterns in species' leaf and fruit phenology. For certain species, the patterns in timing over years in the bubble plots and wide spread in the histograms indicate that within a given year, these species undergo the phenological event at approximately the same time across sites, although year-to-year variation in the timing of the event may be high at a given site. These species include leaf-out in *D. pulchella*, *Scleropogon brevifolius*, and *Muhlenbergia arenacea*, and first fruit in *L. tridentata* and *M. porteri*. In these situations, the variation in site-level conditions could have little influence on the timing of leaf or fruit initiation.

Phenological guilds

Identifying guilds or assemblages of species that share ecological traits is a common practice in ecology (Simberloff and Dayan 1991). Inherent to guilds is the concept of functional redundancy. Functional redundancy has been used to represent cases in which some species perform similar roles in communities and ecosystems (Rosenfeld 2002). It has also been used in the context of biodiversity to reflect that some species may be lost with low impact on ecosystem function (Lawton and Brown 1993). The prospect of having functionally interchangeable species (within a guild) to meet management and conservation planning goals is valuable. In addition, the fact that phenological guilds represent functional responses offers insight for research and management.

We highlight the benefit of phenological guilds to management using the C_4 grass fruit guilds as an example. First, the phenology patterns for C_4 grass fruit guilds 1 and 2 over 23 yr are similar; however, one key difference is in the higher number of instances in the C_4 grass fruit guild 2 to produce no fruit in dry years (represented by Not Obs in bubble plots years 2009, 2011, and 2012). This could indicate higher susceptibility to drought. Second, there are C_4 grass species that occur in both fruit guilds 1 and 2 that represent site-level distinction in phenology patterns over time (i.e., many species at the same site exhibited similar fruiting behavior). The behavioral similarity of species across sites may be useful to the many managers across the western United States who have adopted the ecological site framework for land management (Brown and Bestelmeyer 2016). Ecological sites are conceptual divisions of a landscape that differ from other divisions with respect to biophysical characteristics and potential response to management (Bestelmeyer et al. 2004). Currently, phenology is not explicitly a component of the state-and-transition models that are developed for each ecological site in this conceptual framework (USDA-NRCS 2010); however, such information may be a useful addition as it can inform potential state changes under different climatological patterns.

Ideas for future research

Two factors precluded strong interpretations of cause and effect between environmental variables investigated and the phenology patterns identified. First, phenology is an inherent temporal process. The static nature of the physical site and soil characteristics does not match the temporal resolution of the phenology data. These results clearly illustrate the need to incorporate environmental data expressed over time (e.g., precipitation and soil moisture dynamics; Duniway et al. 2018) to better understand the relationships between sites and species phenology patterns. Second, the monthly sampling interval in this long-term study is coarse relative to changes that may occur over the longer term. However, this study does provide impetus for future research as well as observations that can be used to verify regional and broader scale model predictions of plant phenology in water-limited ecosystems which are governed by more complex dynamics than mesic

systems, where temperature and daylength exert strong effects on phenology (Kemp 1983, Munson and Long 2017). Finally, flowering is not adequately captured via monthly observations made in this arid ecosystem. Flowering phenology exhibited the greatest inter- and intra-specific variation and highest number of clusters per the Mantel test. We believe this reflects the preponderance of missing records in the first flower data matrix. We recommend sample intervals between one to two weeks to capture reproductive phenology focused exclusively on floral resources and/or pollination processes in this arid environment. This recommendation is based on preliminary data from another study that indicates the average time between first flower and fruit is two weeks (D. M. Browning, *unpublished data*).

Management implications

We see three main advantages of describing and understanding phenological guilds for improving land management. First, guilds reduce the number of elements for planning and are based on functional response derived from long-term or contemporary data rather than taxonomic designation. Second, and perhaps more importantly, phenological guilds can facilitate comparison across communities, ecological sites, and ecosystems. Third, predicting phenology of species and groups of species can improve efficiency of ecosystem monitoring, for which available resources are frequently limited. Therefore, it is imperative to select target species or groups of species that exhibit similar phenological patterns in timing and/or responsivity—phenological guilds or phenological functional groups—that can offer the greatest insight into the system's functioning or trajectory. Species or phenological guilds that are insensitive to abiotic conditions and therefore exhibit consistent phenology from year to year are not ideal species to track; these species are likely to only offer useful information if a very dramatic change is occurring. Likewise, species that are observed infrequently or are extremely variable are also not best choices: If a species is observed infrequently, it may take many years to accumulate enough data to be useful. Species or phenological guilds that undergo a phenological event regularly (e.g., in most years) and also appear to be sensitive to environmental conditions can offer the most information.

Identification and use of phenological guilds can potentially improve efficiency in resource allocation for monitoring species phenology for conservation or management objectives and developing predictive models regarding ecosystem drivers for phenological events. Further, recent theoretical works have suggested that systems with high functional redundancy and response diversity are more stable than those with less redundancy (Elmqvist et al. 2003, Mori et al. 2013). Resilience will prove to be especially important in the face of future climate change.

ACKNOWLEDGMENTS

LITERATURE CITED

Allred, K. W. 1983. A field guide to the grasses of New Mexico. Department of Agricultural Communications, New Mexico State University, Las Cruces, New Mexico, USA.

Beatley, J. C. 1974. Phenological events and their environmental triggers in Mojave Desert Ecosystems. Ecology 55:856–863.

Bestelmeyer, B. T., J. E. Herrick, J. R. Brown, D. A. Trujillo, and K. M. Havstad. 2004. Land management in the American Southwest: a state-and-transition approach to ecosystem complexity. Environmental Management 34:38–51.

Boehner, J., R. Koethe, O. Conrad, J. Gross, A. Ringeler, and T. Selige. 2002. Soil regionalisation by means of terrain analysis and process parameterisation. Pages 213–222 in E. Micheli, F. Nachtergaele, and L. Montanarella, editors. Soil classification 2001.

Research Report No. 7, EUR 20398 EN, European Soil Bureau, Luxembourg City, Luxembourg.

Borcard, D., F. Gillet, and P. Legendre. 2011. Numerical ecology with R. Springer, New York, New York, USA.

Brown, J. R., and B. T. Bestelmeyer. 2016. An introduction to the special issue "ecological sites for landscape management". Rangelands 38:311–312.

Browning, D. M., M. C. Duniway, A. S. Laliberte, and A. Rango. 2012. Hierarchical analysis of vegetation dynamics over 71 years: soil-rainfall interactions in a Chihuahuan Desert ecosystem. Ecological Applications 22:909–926.

Browning, D. M., S. Spiegal, R. E. Estell, A. F. Cibils, and R. H. Peinetti. 2018. Integrating space and time: a case for phenological context in grazing studies and management. Frontiers of Agricultural Science and Engineering 5:44–56.

Buisson, E., S. T. Alvarado, S. Le Stradic, and L. P. C. Morellato. 2017. Plant phenological research enhances ecological restoration. Restoration Ecology 25:164–171.

Cardoso, F. C. G., R. Marques, P. C. Botosso, and M. C. M. Marques. 2012. Stem growth and phenology of two tropical trees in contrasting soil conditions. Plant and Soil 354:269–281.

Clarke, K. R., and R. M. Warwick. 2001. Change in marine communities: an approach to statistical analysis and interpretation. Second edition. PRIMER-E Ltd., Plymouth, UK.

Conrad, O., B. Bechtel, M. Bock, H. Dietrich, E. Fischer, L. Gerlitz, J. Wehberg, V. Wichmann, and J. Böhner. 2015. System for automated geoscientific analyses (SAGA) v. 2.1.4. Geoscientific Model Development 8:1991–2007.

Cook, E. R., C. A. Woodhouse, C. M. Eakin, D. M. Meko, and D. W. Stahle. 2004. Long-term aridity changes in the western United States. Science 306:1015–1018.

Correll, D. S., and M. C. Johnston. 1970. Manual of the vascular plants of Texas. Texas Research Foundation, Renner, Texas, USA.

Crimmins, T. M., C. D. Bertelsen, and M. A. Crimmins. 2014. Within-season flowering interruptions are common in the water-limited Sky Islands. International Journal of Biometeorology 58:419–426.

Crimmins, T. M., M. A. Crimmins, and C. D. Bertelsen. 2010. Complex responses to climate drivers in onset of spring flowering across a semi-arid elevation gradient. Journal of Ecology 98:1042–1051.

Crimmins, T. M., M. A. Crimmins, and C. D. Bertelsen. 2013a. Spring and summer patterns in flowering onset, duration, and constancy across a water-limited gradient. American Journal of Botany 100:1137–1147.

Crimmins, T. M., M. A. Crimmins, and C. D. Bertelsen. 2013*b*. Temporal patterns in species flowering in Sky Islands of the Sonoran Desert ecoregion. Pages 33–39 *in* Merging science and management in a rapidly changing world: biodiversity and management of the Madrean Archipelago III. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Tucson, Arizona, USA.

Donnelly, A., and R. Yu. 2017. The rise of phenology with climate change: an evaluation of IJB publications. International Journal of Biometeorology 61: S29–S50.

Duniway, M., M. Petrie, D. Peters, J. Anderson, and J. Herrick. 2018. Soil water dynamics at 15 locations distributed across a desert landscape: insights from a 27 year dataset. Ecosphere 9:e02335.

Elmqvist, T., C. Folke, M. Nystrom, G. Peterson, J. Bengtsson, B. Walker, and J. Norberg. 2003. Response diversity, ecosystem change, and resilience. Frontiers in Ecology and the Environment 1:488–494.

Enquist, C. A. F., J. L. Kellermann, K. L. Gerst, and A. J. Miller-Rushing. 2014. Phenology research for natural resource management in the United States. International Journal of Biometeorology 58:579–589.

Fredrickson, E., K. M. Havstad, and R. Estell. 1998. Perspectives on desertification: south-western United States. Journal of Arid Environments 39:191–207.

Gibbens, R. P., and J. M. Lenz. 2001. Root systems of some Chihuahuan Desert plants. Journal of Arid Environments 49:221–263.

Gibbens, R. P., R. P. McNeely, K. M. Havstad, R. F. Beck, and B. Nolen. 2005. Vegetation changes in the Jornada Basin from 1858 to 1998. Journal of Arid Environments 61:651–668.

Golluscio, R. A., M. Oesterheld, and M. R. Aguiar. 2005. Relationship between phenology and life form: a test with 25 Patagonian species. Ecography 28:273–282.

Gremer, J. R., J. B. Bradford, S. M. Munson, and M. C. Duniway. 2015. Desert grassland responses to climate and soil moisture suggest divergent vulnerabilities across the southwestern United States. Global Change Biology 21:4049–4062.

Gurevitch, J., S. M. Scheiner, and G. A. Fox. 2006. The ecology of plants. Second edition. Sinauer Associates, Sunderland, Massachusetts, USA.

Havstad, K. M., E. L. Fredrickson, and L. F. Huennecke. 2006. Grazing livestock management in an arid ecosystem. Pages 266–277 *in* K. M. Havstad, L. F. Huennecke, and W. H. Schlesinger, editors. Structure and function of a Chihuahuan Desert ecosystem. The Jornada Basin Long-Term Ecological Research Site. Oxford University Press, Oxford, UK.

Herrick, J. E., J. W. Van Zee, K. Havstad, L. M. Burkett, and W. G. Whitford. 2005. Monitoring manual for grassland, shrubland, and savanna ecosystems. USDA-ARS Jornada Experimental Range, Las Cruces, New Mexico, USA.

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 8:247–264.

James, J. J., E. S. Gornish, J. M. DiTomaso, J. Davy, M. P. Doran, T. Becchetti, D. Lile, P. Brownsey, and E. A. Laca. 2015. Managing medusahead (*Taeniatherum caput-medusae*) on rangeland: a meta-analysis of control effects and assessment of stakeholder needs. Rangeland Ecology & Management 68:215–223.

Kaufman, L., and P. J. Rousseeuw. 2009. Finding groups in data: an introduction to cluster analysis. John Wiley and Sons, Hoboken, New Jersey, USA.

Kemp, P. R. 1983. Phenological patterns of Chihuahuan Desert plants in relation to timing of water availability. Journal of Ecology 71:427–436.

Kurc, S. A., and L. M. Benton. 2010. Digital image-derived greenness links deep soil moisture to carbon uptake in a creosotebush-dominated shrubland. Journal of Arid Environments 74:585–594.

Lawton, J. H., and V. K. Brown. 1993. Redundancy in ecosystems. Pages 255–270 *in* E. D. Schulze and H. A. Mooney, editors. Biodiversity and ecosystem function. Springer, Springer Berlin Heidelberg, Berlin, Germany.

Mazer, S. J., K. L. Gerst, E. R. Matthews, and A. Evenden. 2015. Species-specific phenological responses to winter temperature and precipitation in a water-limited ecosystem. Ecosphere 6:98.

MEA [Millennium Ecosystem Assessment]. 2005. Ecosystems and human well-being: desertification synthesis. World Resources Institute, Washington, D.C., USA.

Mori, A. S., T. Furukawa, and T. Sasaki. 2013. Response diversity determines the resilience of ecosystems to environmental change. Biological Reviews 88:349–364.

Morisette, J. T., et al. 2009. Tracking the rhythm of the seasons in the face of global change: phenological research in the 21st century. Frontiers in Ecology and the Environment 7:253–260.

Munson, S. M., and A. L. Long. 2017. Climate drives shifts in grass reproductive phenology across the western USA. New Phytologist 213:1945–1955.

Noy-Meir, I. 1973. Desert ecosystems: environment and producers. Annual Review of Ecology and Systematics 4:25–51.

Oksanen, J. F., et al. 2018. Package vegan: community ecology package. Cran.r-project.org. https://cran.r-project.org/web/packages/vegan/vegan.pdf

Parmesan, C., and G. Yohe. 2003. A globally coherent fingerprint of climate change impacts across natural systems. Nature 421:37–42.

Pavon, N. P., and O. Briones. 2001. Phenological patterns of nine perennial plants in an intertropical semi-arid Mexican scrub. Journal of Arid Environments 49:265–277.

Peters, D. P. C., B. T. Bestelmeyer, J. E. Herrick, E. L. Fredrickson, H. C. Monger, and K. M. Havstad. 2006. Disentangling complex landscapes: new insights into arid and semiarid system dynamics. BioScience 56:491–501.

Peters, D. C., J. Yao, D. M. Browning, and A. Rango. 2014. Mechanisms of grass response in grasslands and shrublands during dry or wet periods. Oecologia 174:1323–1334.

Peters, D. P. C., J. Yao, O. E. Sala, and J. P. Anderson. 2012. Directional climate change and potential reversal of desertification in arid and semiarid ecosystems. Global Change Biology 18:151–163.

Pezzani, F., and C. Montana. 2006. Inter- and intraspecific variation in the germination response to light quality and scarification in grasses growing in two-phase mosaics of the Chihuahuan Desert. Annals of Botany 97:1063–1071.

Pfister, C., G. SchwarzZanetti, and M. Wegmann. 1996. Winter severity in Europe: the fourteenth century. Climatic Change 34:91–108.

Primack, R. B., and A. J. Miller-Rushing. 2011. Broadening the study of phenology and climate change. New Phytologist 191:307–309.

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 169:156–173.

Root, R. B. 1967. Niche exploitation pattern of Blue-Gray Gnatcatcher. Ecological Monographs 37:317.

Rosenfeld, J. S. 2002. Functional redundancy in ecology and conservation. Oikos 98:156–162.

Seghieri, J., et al. 2009. Relationships between climate, soil moisture and phenology of the woody cover in two sites located along the West African latitudinal gradient. Journal of Hydrology 375:78–89.

Sherry, R. A., X. H. Zhou, S. L. Gu, J. A. Arnone, D. S. Schimel, P. S. Verburg, L. L. Wallace, and Y. Q. Luo. 2007. Divergence of reproductive phenology under climate warming. Proceedings of the National Academy of Sciences USA 104:198–202.

Simberloff, D., and T. Dayan. 1991. The guild concept and the structure of ecological communities. Annual Review of Ecology and Systematics 22:115–143.

Syvertsen, J. P., G. L. Nickell, R. W. Spellenberg, and G. L. Cunningham. 1976. Carbon reduction pathways and standing crop in C3 Chihuahuan Desert plant communities. Southwestern Naturalist 21: 311–320.

USDA-NRCS [U.S. Department of Agriculture, Natural Resource Conservation Service]. 2010. Ecological site information system. National Resource Conservation Service, Lincoln, Nebraska, USA.

Wainwright, J. 2006. Climate and Climatological Variations in the Jornada Basin. Pages 44–80 in K. M. Havstad, L. F. Huennecke, and W. H. Schlesinger, editors. Structure and function of a Chihuahuan Desert ecosystem. The Jornada Basin Long-Term Ecological Research Site. Oxford University Press, Oxford, UK.

Ward, J. H. 1963. Hierarchical grouping to optimize an objective function. Journal of the American Statistical Association 58:236–244.

Wheeler, C. A., J. B. Bettaso, D. T. Ashton, and H. H. Welsh. 2015. Effects of water temperature on breeding phenology, growth, and metamorphosis of Foothill Yellow-Legged frogs (Rana boylii): a case study of the regulated mainstream and unregulated tributaries of California's Trinity River. River Research and Applications 31:1276–1286.

Wolkovich, E. M., and E. E. Cleland. 2011. The phenology of plant invasions: a community ecology perspective. Frontiers in Ecology and the Environment 9:287–294.

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