

**DIFFERENCES IN THE TIMING OF GERMINATION AND REPRODUCTION
RELATE TO GROWTH PHYSIOLOGY AND POPULATION DYNAMICS OF
SONORAN DESERT WINTER ANNUALS¹**

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- *Premise of the Study:* Trait differences can promote distinct survival and fecundity responses to environmental fluctuations. In a Sonoran Desert winter annual plant community, we have identified a tradeoff between relative growth rate (RGR) and water-use efficiency (WUE) that predicts interannual variation in reproductive success. Here we test the hypothesis that traits underlying RGR and WUE differences are linked to seasonal phenology.
- *Methods:* We use long-term demographic data and finer-scale, short-term data to investigate timing of germination, reproduction, and death of several winter annual species in multiple years in open and under-shrub habitats. We hypothesized that species with high WUE and less interannual demographic variability would have life cycle transitions early in the winter to spring growing season. This would be due to an ability to use small amounts of rain and photosynthesize at low temperatures. By contrast, we hypothesized that species with low WUE whose survival and reproductive rates vary greatly from year to year would have life cycle transitions later in the season.
- *Key Results:* In any given year, species with high WUE germinated and reproduced earlier in the season than species with low WUE, whereas low-WUE species germinated later and had shorter reproductive phases.
- *Conclusions:* Our results demonstrate a direct relationship between phenology and physiological trait differences. This link between phenology and physiology is of interest because it clarifies the mechanism by which trait differences determine species' relative abundances.

Key words: desert annuals; germination; phenology; population dynamics; relative growth rate; water-use efficiency.

Seed germination is a risky life history transition because newly germinated seedlings are successful only when postgermination environmental conditions are favorable (Baskin and Baskin, 1998; Finch-Savage et al., 2007). Species exhibit a variety of seed dormancy mechanisms, presumably as a result of different selective pressures in a range of habitats, and environmental cues that trigger germination also vary by species (Baskin and Baskin, 1998; Finch-Savage and Leubner-Metzger, 2006). Species differ in the time required for wetted nondormant seeds to germinate, and longer germination times may be an adaptation to prevent germination under unfavorable conditions, especially in arid regions (Kos and Poschlod, 2010). As a result, species differ in their timing of germination, which may influence their synchrony with favorable growing conditions, their exposure to competition and predation, and community structure (Forbis, 2010; Kos and Poschlod, 2010). Likewise, the timing of growth and reproduction differs among species,

reflecting unique physiological adaptations for resource utilization under particular environmental conditions (Pavon and Briones, 2001). Timing of growth and reproduction of annual plants in arid environments is especially critical because seed production and resource allocation must be completed before conditions become too harsh for survival (Jackson and Bliss, 1984).

Desert annual plant communities experience high variation in the amount and timing of precipitation (Beatley, 1974; Chesson and Huntly, 1989; Pake and Venable, 1996; Adondakis and Venable, 2004). Variable environmental conditions result in interannual variability in germination, survival, and fecundity of annual plants (Beatley, 1967; Adondakis and Venable, 2004; Venable and Kimball, 2010). In a Sonoran Desert winter annual system, we have documented a tradeoff between relative growth rate (RGR) and water-use efficiency (WUE), such that species with high RGR had low WUE and vice versa (Angert et al., 2007; Huxman et al., 2008). The position of species along the RGR–WUE tradeoff has been related to variation in reproductive success from year to year (Angert et al., 2007, 2009). Demographically variable species (those with greater yearly variation in per capita rates of survival and seed production, calculated as the geometric standard deviation of per capita survival multiplied by per capita seed production) have high RGR and low WUE, whereas demographically buffered species (those that experienced less interannual demographic variability) have low RGR and high WUE. Angert et al. (2009) used this system to quantify the magnitude of coexistence promoting

¹Manuscript received 21 January 2011; revision accepted 17 August 2011.

Funding was provided by NSF grants BSR 9107324, DEB 9419905 (LTREB), DEB 0212782 (LTREB) DEB 0717466 (LTREB), 0817121 (LTREB) to DLV, DEB 0453781 to DLV & TEH, and DEB 0717380 to ALA, DLV & TEH. The Phileology Foundation of Fort Worth Texas provided additional support.

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storage effect and to demonstrate that species differences in physiology are correlated with species differences in the survival and reproduction in response to environmental variation (species \times year interaction for per germinant fecundity, calculated as per capita survival multiplied by per capita seed production) that underlies the storage effect. Thus, there is a direct relationship among functional traits, population dynamics, and species coexistence (Angert et al., 2007, 2009; Huxman et al., 2008).

The demographically variable, low WUE–high RGR species are more sensitive to interannual changes in total growing season precipitation and achieve high reproductive rates during years with large rain events, whereas the demographically buffered, high WUE–low RGR species maintain more constant reproductive rates, even during years with small rain events and warm temperatures late in the growing season (Venable, 2007; Kimball et al., 2011). The buffered species have been shown to have high investment in light-harvesting photosynthetic capacities, which can increase carbon gain at low temperatures (Huxman et al., 2008). This suggests possible species differences in the timing of photosynthesis. Demographically buffered species may be better able to photosynthesize during relatively cool periods early in the January–May growing season, immediately after pulses of precipitation, or early in the morning (Huxman et al., 2008). Species may also respond to differences in temperature and moisture at the microhabitat level. For example, demographically buffered, high WUE species may also have earlier phenology under the cover of creosote shrubs, where temperatures are lower than in open habitats (Pake and Venable, 1995).

Here, we explore whether the functional traits associated with demographically buffered species are also associated with early seasonal phenology. We want to determine how physiological trait differences result in species differences in survival and reproductive traits. This is important because different demographic responses of species to varying environmental conditions determine community composition through time. We use long- and short-term phenological data for Sonoran Desert winter annuals to address the following questions: (1) Do species differ in timing of germination, reproduction, and senescence? (2) Are phenological differences related to the previously identified physiological trait differences that affect population dynamics? And (3) Does germination phenology vary depending on habitat (open vs. under-shrub environments)? We hypothesized that species with high WUE (demographically buffered species) would have earlier phenology because of their ability to photosynthesize at low temperatures during winter and spring (Huxman et al., 2008). We also hypothesized that phenology might differ depending on habitat because a previous study indicated that these two habitats differed in terms of temperature and soil type (Pake and Venable, 1995) and because microhabitat has been shown to cause small but statistically significant differences in growth and allocation within some of these species (Angert et al., 2007).

MATERIALS AND METHODS

Long-term censuses—Germination, survival, and fecundity of desert winter annuals have been recorded annually in permanently marked plots from the 1982–1983 winter growing season through the present (Venable, 2007). The plots are located at the University of Arizona Desert Laboratory in Tucson, Arizona, USA, along a 250-m transect in a creosote flat that has been protected

from grazing since 1907. Each year, plots were first visited ca. 10 d after every autumn and winter rain event to record germination. Plots were revisited at roughly monthly intervals or following subsequent rain events that might trigger further germination. All individuals in each plot were mapped and reproduction and mortality were recorded until senescence at the end of the growing season. Paired plots were later established under the cover of creosote shrubs (*Larrea tridentata*) because this is the dominant shrub at our site, creating a habitat mosaic of ca. 50% cover. There are now a total of 72 plots: half are located in the open and half are under shrubs. To examine species main effects we analyzed open plots from the 1982–1983 season to the 2008–2009 season, and to examine habitat effects we compared data in open and under-shrub plots from the 1994–1995 season to the 2008–2009 season.

Study system, physiological traits—In 2004–2005, a study was conducted to measure physiological traits of nine focal species for which there are long-term records from the censuses and that differ in their degree of interannual demographic variability (Angert et al., 2007, 2009; Huxman et al., 2008). Here, we summarize how these previously published results were obtained because we use them in the present study to investigate how physiology is related to phenology. To determine RGR and patterns of biomass allocation, one or two individuals of each species were harvested every 2 wk throughout the growing season from 30 random sampling points along the same 250 m transect as the long-term plots. After transport to the laboratory, harvested plants were separated into root, leaf, stem, and reproductive biomass. During February and March of 2005, carbon assimilation (A) and internal CO_2 concentration (C_i) were measured with a Li-Cor 6400 portable photosynthesis system (Li-Cor, Lincoln, Nebraska, USA). The CO_2 concentration in the cuvette was varied to construct A – C_i curves from which V_{Cmax} (maximum rate of carboxylation by Rubisco) and J_{max} (light-saturated rate of electron transport) were calculated. Leaves were analyzed for their carbon isotope ratios to determine the degree of carbon isotope discrimination, Δ , which is a measure of WUE over the lifetime of the leaf (Farquhar et al., 1989). The same leaves were used to measure N content. Physiological traits were combined by principal component analysis into a single variable, “physiological PC1,” which included integrated specific leaf area (area under the curve of specific leaf area vs. time), integrated leaf mass ratio, RGR responsiveness (relative change in RGR surrounding the mid-season rain event), $J_{\text{max}}:V_{\text{Cmax}}$, and leaf N. PC1 captures 54% of the variation in the original variables and captures the tradeoff between traits yielding high WUE and traits yielding high RGR. High PC1 scores indicate high WUE and low RGR, whereas low PC1 scores correspond to the opposite pattern. Note that the PC1 axes in Huxman et al. (2008) and Angert et al. (2009) represent the same variables but that the sign of the PC1 scores is reversed such that high PC1 refers to high RGR in those papers. The sign flipped when the calculations were re-done on slightly different data (including versus excluding non-native species) but the relative position of species is the same. PC1 is a useful metric because it simplifies the complexity in physiological trait variation, collapsing many traits onto one axis. More details regarding these measurements of physiological traits and their incorporation into physiological PC1, as well as additional results from these measurements, can be found in Huxman et al. (2008) and Angert et al. (2009).

Germination phenology—To understand germination phenology, we focus on the nine winter annual plant species for which we have detailed physiological data (Table 1). These species are a taxonomically diverse group, representing a range of different families and including two species not native to the study area. They were selected because they are the most abundant species in the long-term censuses and they have different long-term demographic patterns. We used the long-term demographic data set (from the 1982–1983 season through the 2008–2009 season) to analyze germination phenology, first including only the open-habitat plots, because those are the ones for which we have the most years of data. The test for habitat differences (below) included both the open-habitat and under-shrub plots from 1993–1994 to 2008–2009. For each year, we calculated the average date of germination for each species and put the species in rank order of germination date. Rank order of average germination date was analyzed by analysis of variance (ANOVA) with species as a fixed factor. For more fine-scaled data, we also analyzed the recorded date of germination of all individuals of the nine focal species in all plots and all years. We used mixed-model ANOVA with species as the fixed factor and plot, year, and species \times year interaction as random factors. We supplemented the ANOVA with Tukey post hoc comparisons to test for differences among the species. Next we tested the hypothesis that the timing of germination is related to physiological and demographic traits. We did this by correlating the estimated

TABLE 1. The nine focal species (selected for their abundance and the availability of long-term demographic data and physiological trait data), alternative species names, abbreviations, whether they are native to the Sonoran Desert, their family, their estimated average date of germination, the standard error (SE) of the estimate, and results of a Tukey post hoc test. Species that share the same letters are not significantly different from each other. Species are listed in order of their germination date.

Species	Alternative species names	Abbreviation	Native?	Family	Date	SE	Tukey
<i>Erodium cicutarium</i>		erci	No	Geraniaceae	7-Dec	6.4013	C
<i>Erodium texanum</i>		erte	Yes	Geraniaceae	10-Dec	6.4631	BC
<i>Plantago insularis</i>	<i>Plantago ovata</i>	plin	Yes	Plantaginaceae	10-Dec	6.4214	BC
<i>Schismus barbatus</i>		scha	No	Poaceae	10-Dec	6.3732	BC
<i>Pectocarya recurvata</i>		pere	Yes	Boraginaceae	12-Dec	6.3709	ABC
<i>Plantago patagonica</i>	<i>Plantago purshii</i>	plpa	Yes	Plantaginaceae	13-Dec	6.3845	ABC
<i>Eriophyllum lanosum</i>	<i>Antheropeas lanosum</i>	erla	Yes	Asteraceae	18-Dec	6.419	AB
<i>Sytlocline micropoides</i>		stmi	Yes	Asteraceae	18-Dec	6.4882	AB
<i>Evax multicaulis</i>	<i>Evax verna</i> , <i>Diaperia verna</i>	evmu	Yes	Asteraceae	20-Dec	6.4499	A

germination date for each species from the ANOVA (least squares means) and the species average rank order of germination date with physiological PC1, WUE, RGR, demographic variability (the geometric standard deviation of per germinant fecundity) and average germination fraction (the number of germinated seedlings divided by the number of viable seeds left in the soil plus germinated seedlings, averaged from 1990 to 2007). Although we tested the relationship with both WUE and RGR (the two physiological traits that trade off with each other), we also tested for a relationship with physiological PC1, the metric that includes multiple traits that underlie WUE and RGR.

Reproductive phenology—The long-term data set does not include detailed information on differences among species in the timing of reproduction, so we addressed this question with data on the timing of reproduction collected for the 2004–2005 growing season. We hypothesized that high-WUE species would reproduce earlier than low-WUE species because of their ability to photosynthesize at low temperatures. In 2004–2005, all plants germinated in response to a single rain event, so they all belong to the same germination cohort. This allowed us to be sure that any differences among species in the timing of reproduction were not influenced by differences in the timing of germination. In each of the 2004–2005 study plots (see *Study system, physiological traits*), we noted the date on which reproductive material was first and last collected for each species. We performed two one-way ANOVAs to determine whether the date of first reproduction and the number of days spent reproducing varied with species. We then used correlation to determine whether the average date of first reproduction and the average number of days spent reproducing were related to physiological PC1 (the first principal component score for physiological traits), WUE, RGR, demographic variability, and average germination fraction.

Death—We hypothesized that high-WUE species would have earlier death dates than low-WUE species. To investigate timing of death we used the death date of each individual from the long-term data set (open-habitat plots only). We expected that death date would be influenced by germination date, so we also calculated the life span of each individual by subtracting germination date from death date. Death date was noted as either the first census date on which a plant was found to be dead or, if the plant was still alive on the final reproductive census, date of death was estimated to be 2 wk later than the date of this last census. The 2-wk assumption is reasonable because the last census date occurs when temperatures approach or surpass 38°C, which we know from experience signals the end of the season and the death of annuals. Because censuses were systematically conducted only following each germination-inducing rain early in the season and roughly monthly thereafter, data on timing of death are less resolved than data on timing of germination. We performed two separate mixed-model ANOVAs (one for date of death and one for life span) with species as a fixed factor and plot, year, and species \times year interaction as random factors. We used correlation to explore the relationship of physiology and demographic variability to estimated life span and death date.

Phenology and habitat, 2007–2008 growing season—Detailed germination, reproductive, and death phenology data were collected in plots during the 2007–2008 growing season. We established thirty-two 20 \times 20 cm plots at the Desert Laboratory near the long-term plots (located along a ca. 10 m transect located ca. 5–10 m away from the previously established plots). Sixteen plots were placed under creosote shrubs and paired with 16 in nearby open habitats.

Beginning 1 wk following the first winter rain event on 29 November, germination, survival, and the phenological stage of all plants were noted every 1–2 wk. The date on which each individual first germinated, developed flowers, developed mature fruits, and died was analyzed by mixed-model ANOVA with species and habitat (open or under-shrub) as fixed factors and plot as a random factor. Date of germination may influence the date on which subsequent phenological stages are reached, so we also calculated the number of days from germination until flowering, from germination until the production of mature fruits, and from germination until death (the life span) for each individual and analyzed these periods by mixed-model ANOVA with species and habitat (open or under-shrub) as fixed factors and plot as a random factor. Tukey post hoc comparisons were used to test for differences among species. This method of analysis is appropriate for our data because we do not have any censored data and the residuals were approximately normally distributed. We tested for a correlation between the average date that each phenological stage was reached and physiological PC1 for the seven species with physiological data that germinated in these plots. To determine whether any differences between phenology in open versus shrub plots were related to physiology, the mean date at which each phenological stage was reached under shrubs was subtracted from the mean value in the open. The resulting values were correlated with physiological PC1. Soil temperature and moisture probes were placed in an open area and under a shrub at the soil surface and at 10 cm depth and readings were taken every 15 min throughout the germination season (Onset Computer Corp., Bourne, Massachusetts, USA).

Phenology and habitat, long-term data—For our nine focal species, we also used data from the paired open and shrub plots from 1994–1995 to 2008–2009 of the long-term data set to investigate the influence of open and under-shrub habitats on phenology. We analyzed germination, death date, and life span (death date minus germination date) with separate ANOVAs. We used mixed-model ANOVA with species, habitat, and species \times habitat as fixed factors and plot, year, year \times habitat, species \times year, and species \times year \times habitat as random factors. We supplemented the ANOVA with Tukey post hoc comparisons to test for differences among species and habitats. We subtracted the estimated date (least squares means from the ANOVAs, the main effect of species after removing the effects of plot and year) at which each phenological stage was reached under shrubs from the estimated value in the open and correlated the resulting values with physiological PC1 to determine whether there were differences between phenology in open versus shrub plots that were related to physiology.

RESULTS

Germination phenology—Using 25 yr of field data, we found that both rank order and calendar date of germination differed among species, with some species, such as *Erodium cicutarium*, tending to germinate earlier than others, such as *Evax multicaulis* and *Sytlocline micropoides* (Table 1; rank order of germination $F_{8,140} = 7.98$, $P < 0.0001$; estimated date of germination $F_{8,140} = 4.43$, $P < 0.0001$). As we hypothesized, species with high physiological PC1 scores (characterized by high WUE and low RGR) germinated earlier than species with low

TABLE 2. Long-term data: r and P values from correlations comparing the relationships between timing of germination and timing of death to physiological PC1, water-use efficiency (WUE, as measured by Δ), relative growth rate (RGR), demographic variability, and germination fraction. Demographic variability is the geometric standard deviation of per germinant fecundity (survival from germination to reproduction multiplied by average seed set of survivors). PC1 is the physiological PC score (described in Materials and Methods; ranges from low WUE and high RGR to high WUE and low RGR). Δ is a measure of carbon isotope discrimination, indicating intrinsic WUE, where lower values indicate higher WUE (Farquhar et al., 1989). Germination fraction is the proportion of the soil seed bank that germinates, calculated as the number of seedlings in a given year divided by the number of seeds left dormant in the soil after germination plus the number of seedlings. The germination fraction here is an average of values from 1990 to 2007 (Venable, 2007).

Independent variables	r	P
Rank order of germination		
PC1	-0.79	0.011
Δ (measure of WUE)	0.912	0.001
RGR	0.514	0.157
Demographic variability	0.657	0.054
Germination fraction	-0.698	0.037
Estimated date of germination		
PC1	-0.752	0.019
Δ (measure of WUE)	0.899	0.001
RGR	0.358	0.344
Demographic variability	0.585	0.098
Germination fraction	-0.645	0.061
Estimated life span		
PC1	0.757	0.018
Δ (measure of WUE)	-0.784	0.013
RGR	-0.433	0.244
Demographic variability	-0.759	0.018
Germination fraction	0.789	0.011
Estimated death date		
PC1	0.386	0.305
Δ (measure of WUE)	-0.335	0.378
RGR	-0.281	0.463
Demographic variability	-0.633	0.067
Germination fraction	0.641	0.062

physiological PC1 scores (Table 2 and Fig. 1). Early germination was associated with high overall germination fraction (Table 2). Earlier germination was also associated with warmer temperatures in most years (Fig. 2).

Reproductive phenology—During the 2004–2005 growing season, species differed in the date that they began to produce reproductive structures ($F_{8,272} = 15.986$, $P < 0.0001$). High-WUE species began reproducing earlier than low-WUE species ($r = -0.810$, $P = 0.008$; Fig. 1C), supporting our hypothesis that species with high WUE would have earlier reproduction. The species also differed in the number of days spent reproducing ($F_{9,288} = 16.441$, $P < 0.0001$). High-WUE species reproduced for a longer period than low-WUE species ($r = 0.690$, $P = 0.040$; Fig. 1D).

Death—The 25-yr data set indicated that the date of death did not differ by species ($F_{8,164} = 0.89$, $P = 0.5298$), although they did have significantly different life spans ($F_{8,157} = 5.51$, $P < 0.0001$; Fig. 1E, F). Death date and life span were highly correlated ($r = 0.781$, $P < 0.0001$). The date of death was not related to physiology (PC1, Δ , RGR; Table 2), but species with high physiological PC1 scores (high WUE and low RGR) lived longer than those with low physiological PC1 scores (low WUE and high RGR;

Table 2). Demographically variable species had shorter lives than demographically buffered species (Fig. 1F and Table 2), primarily because of later germination. Germination date was negatively correlated with life span ($r = -0.374$, $P < 0.0001$).

Phenology and habitat, 2007–2008—Twenty-nine species germinated in the 2007–2008 phenology plots. The 21 species found in four or more plots included only seven of the nine focal species for which we have detailed functional trait data (Appendix S1; see Supplemental Data with the online version of this article). Species reached every phenological stage (germination, production of flowers and fruits, and death) at significantly different times and also differed in the number of days between germination and each subsequent phenological stage (Fig. 3 and Table 3). There was no significant main effect of habitat for any of the stages or days between stages, but there was a significant species \times habitat interaction for all phenological stages except for the date of death. These interactions reflected that some species, such as *Pectocarya recurvata*, germinated and reproduced first in the open, whereas others, such as *Cryptantha angustifolia* and *Lepidium lasiocarpum*, germinated and reproduced first under shrubs (online Appendix S2). Similarly, for some species, like *Stylocline micropoides*, the number of days between germination and reproduction was smaller in the open than under shrubs, whereas for others, like *Eucrypta micrantha*, the number was smaller under shrubs (online Appendix S3). *Monoptilon bellioides* is an example of a species that lived longer in the open than under shrubs, whereas *Lepidium lasiocarpum* and other species lived longer under shrubs than in the open (Appendix S3). There was no apparent relationship between the average date on which each phenological stage was reached and physiological PC1 for this year ($P > 0.16$ for all phenological variables, $n = 7$), possibly because of low sample sizes caused by low germination of these species in this year. However, for species that were found in both open and shrub plots in this year (and for which we have physiological data), there was a significant relationship between PC1 and shrub minus open germination date ($r = 0.962$, $P = 0.002$, $n = 6$), which indicates that demographically buffered, high-WUE species germinated first in the open, whereas demographically variable, low-WUE species germinated first under shrubs (Appendix S2). There was no significant relationship between PC1 and habitat differences in the date on which other phenological stages were reached (flowers $r = 0.153$, $P = 0.772$; mature fruit $r = 0.054$, $P = 0.912$; death $r = 0.421$, $P = 0.347$; Appendix S2).

Surface air temperature was more extreme in the open than under shrubs (online Appendix S4A). Maximum daily air temperature averaged 5.9°C warmer and minimum daily air temperature averaged 1.3°C cooler in the open. Additionally, the open-habitat soil was drier, both on the surface and at 10 cm depth as compared to under shrubs (Appendix S4B, C). After the first winter rain event, daily maximum soil moisture averaged 0.04 m³/m³ drier, and minimum soil moisture averaged 0.05 m³/m³ drier in open habitats.

Phenology and habitat, long-term data—From 1994–1995 to 2008–2009, some species germinated a bit earlier in the open whereas other species germinated first under shrubs, but the differences were not strong or significant (species \times habitat $F_{8,145} = 0.28$, $P = 0.97$; Fig. 4A). The relationship between shrub minus open germination date and PC1 was not quite

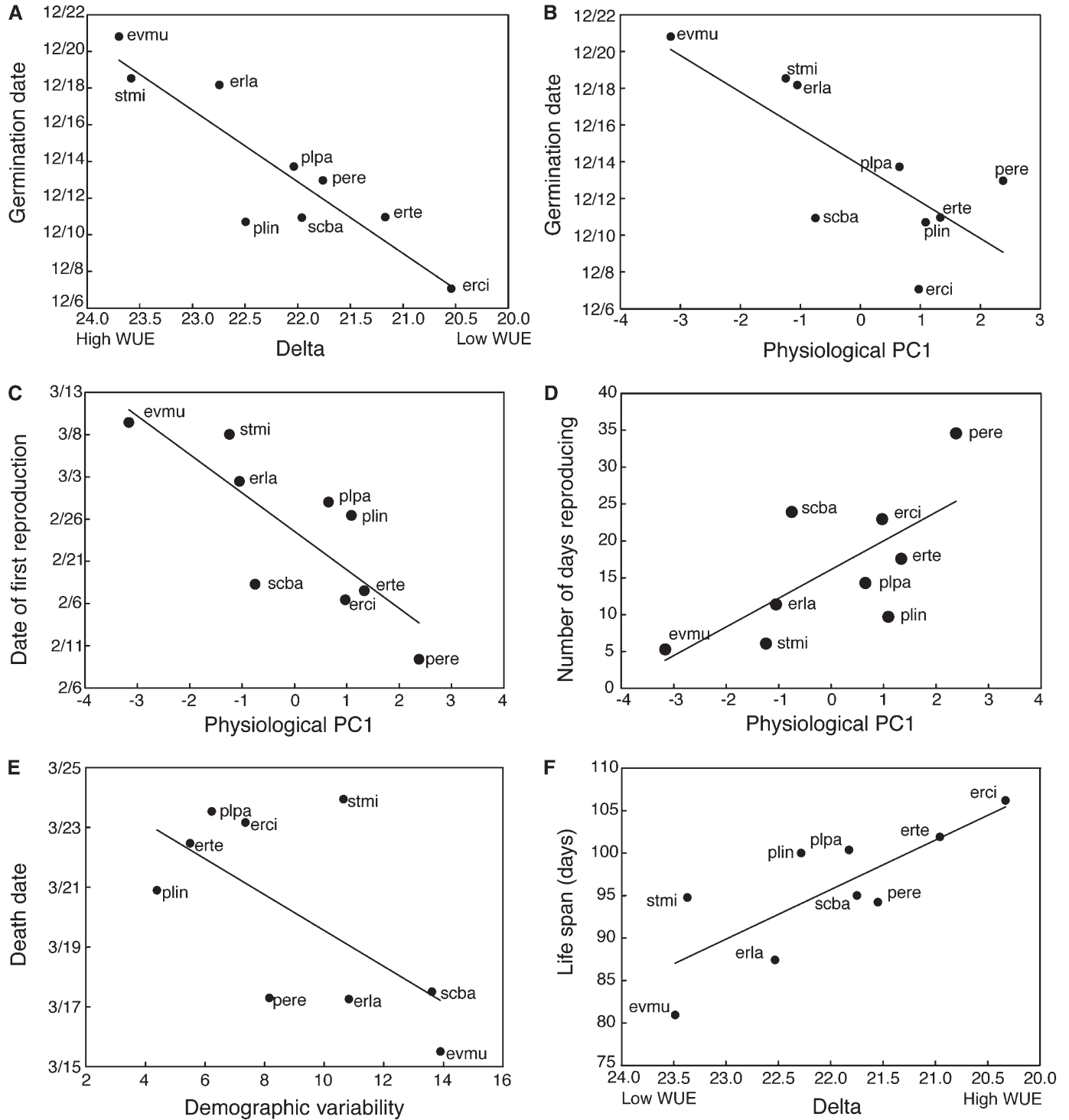


Fig. 1. Correlations between phenology, carbon isotope discrimination, Δ (a measure of WUE), physiological PC1 (position on the RGR–WUE tradeoff), and demographic variability (the geometric standard deviation of fitness). Species with low physiological PC1 scores have high RGR and low WUE. (A) Germination date and Δ from 1982 to 2008. (B) Germination date and physiological PC1 from 1982 to 2008. (C) Average date that each species began producing reproductive material and PC1. (D) Number of days spent reproducing during the 2004–2005 growing season and PC1. (E) Average death date from 1982 to 2009 and demographic variability. (F) Average life span from 1982 to 2009 and Δ .

significant ($r = 0.609$, $P = 0.082$) but followed the same general trend as the 2007–2008 data, with high-WUE species tending to germinate first in the open and low-WUE species tending to germinate first under shrubs. The species germinated at differ-

ent times ($F_{8,144} = 3.76$, $P = 0.0005$) but there was no main habitat effect ($F_{1,14.3} = 0.09$, $P = 0.7704$). This result is qualitatively similar to what we saw with the detailed germination data from 2007–2008 (Table 3). All species lived longer in the open than

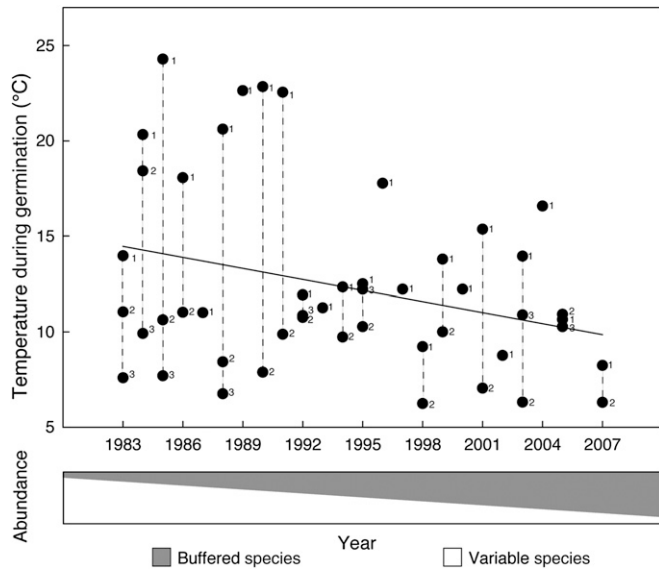


Fig. 2. Temperatures during germination of different cohorts in different years from 1982 to 2008. Mean temperature during and for 5 d following germination-triggering rain events. Dotted lines connect germination events that occurred during the same year. Numbers next to individual dots indicate the order of germination of the different cohorts from early to late. The conceptual diagram (below) indicates the change in community composition over time (Kimball et al., 2010). Buffered species germinate first, under warmer temperatures, in any given year. However, their abundance has increased over time and germination has been occurring under cooler temperatures over time, so buffered species germinate under cooler temperatures than variable species when averaged over all 25 yr.

they did under shrubs (life span ANOVA: species $F_{8,82.7} = 3.57$, $P = 0.0013$; habitat $F_{1,21.8} = 13.78$, $P = 0.0012$; species \times habitat $F_{8,63.4} = 2.28$, $P = 0.0326$; Fig. 4B, C). All species also died at a later date in the open than under shrubs ($F_{1,25.1} = 20.87$, $P < 0.0001$), but by slightly different amounts (species \times habitat $F_{8,68.9} = 1.98$, $P = 0.0618$). The species did not differ in their average death dates ($F_{8,84.8} = 0.91$, $P = 0.5101$). There was no relationship between PC1 and shrub minus open death date or life span ($P > 0.4$ for both variables).

DISCUSSION

Phenological differences and physiological traits—In this Sonoran Desert winter annual community, we found differences in the timing of germination and reproduction that were related to position along a tradeoff between WUE and RGR. High-WUE species in this community are known to have a greater investment in RuBP regeneration capacity, which in part confers a greater ability to photosynthesize in low temperatures (Huxman et al., 2008). We found that these physiological adaptations to dry and cool conditions are associated with a shift to earlier seasonal phenology. Early-germinating species started reproducing early and continued to reproduce for a longer period, possibly because of their low RGR and high WUE.

Germination cues are critical for the success of annual plants, and species should germinate in greater numbers following rain events that promote high survival and reproduction (Venable and Lawlor, 1980). High-WUE, cold-adapted species germinate readily, often after the first rainfall event of the season.

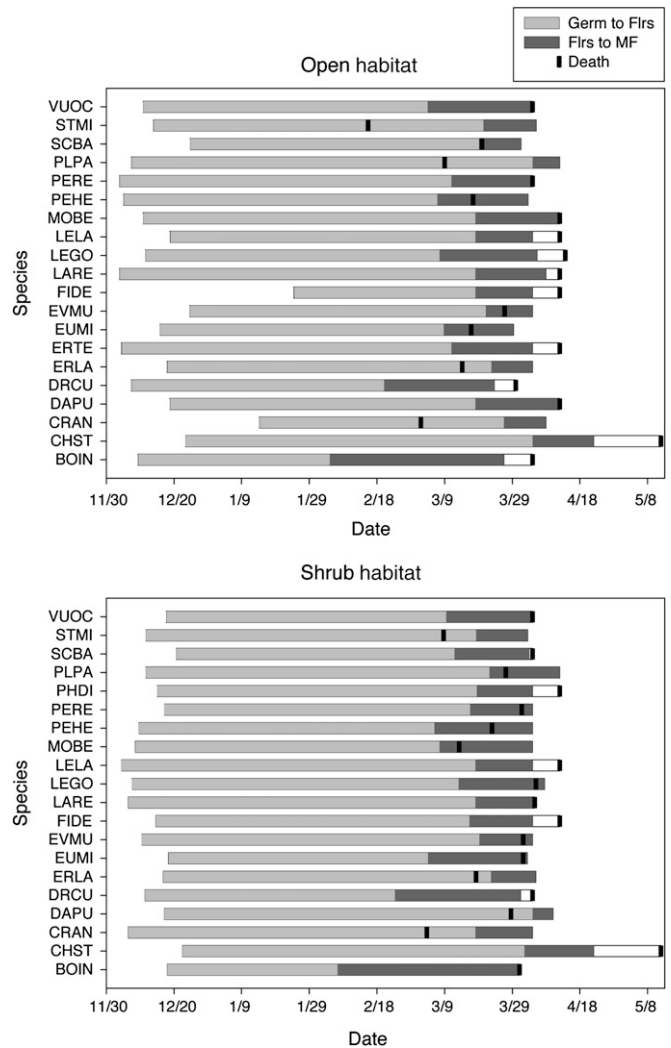


Fig. 3. The mean date that species germinated, produced mature fruit, and died in plots during the 2007–2008 season. Full species names are listed in Appendix S1 in the same (alphabetical) order. Note that some species had high mortality prior to reproduction, so their mean death date is earlier than the date of flowering.

Earlier germination has the potential to expose the plants to warmer conditions during the October–January germination season (Fig. 2). However, this early germination positions them to conduct much of their growth and reproduction relatively early in the January–April growing season, when temperatures are cooler and mortality risks are lower (Beatley, 1974; Venable and Pake, 1999; Bowers, 2005). By contrast, low-WUE, demographically variable species are more likely to germinate following later rainfall events and grow to reproduce during warmer, late growing-season conditions. Under these warmer conditions the risk of mortality is greater, but there is a possibility of attaining greater reproductive success because of high growth rates in favorable years (Went, 1949; Huxman et al., 2008).

Phenology and physiological traits such as WUE have been found to be heritable and to evolve rapidly in response to environmental fluctuations in many systems (Heschel and Riginos, 2005; Donovan et al., 2007; Franks et al. 2007; Kudoh et al.,

TABLE 3. Phenology and habitat, 2007–2008: F and df values from mixed-model ANOVAs comparing the effects of species, habitat, and the species \times habitat interaction on timing of germination, flower production, mature fruit production, death, number of days between germination and flowering, days between germination and mature fruit production, and days alive (from germination to death). Plot was included as a random factor in the analyses. * $P < 0.05$, ** $P < 0.0001$.

Phenological stage	Species	Habitat	Interaction
Germination	$F_{20,1011} = 4.22^{**}$	$F_{1,1015} = 1.9$	$F_{18,1010} = 2.13^*$
Flowers	$F_{20,849} = 63.94^{**}$	$F_{1,851} < 0.01$	$F_{18,847} = 2.37^*$
Mature fruits	$F_{20,851} = 19.92^{**}$	$F_{1,852} = 0.01$	$F_{18,849} = 1.78^*$
Death	$F_{20,1010} = 8.37^{**}$	$F_{1,1013} = 0.32$	$F_{18,1008} = 1.49$
Days from germination to flowering	$F_{20,832} = 6.75^{**}$	$F_{1,848} = 1.50$	$F_{18,849} = 2.25^*$
Days from germination to mature fruits	$F_{20,853} = 4.84^{**}$	$F_{1,858} = 1.69$	$F_{18,854} = 2.10^*$
Days alive	$F_{20,1010} = 7.12^{**}$	$F_{1,1014} = 0.10$	$F_{18,1009} = 1.95^*$

2007). Although it is unclear whether phenology evolved as a result of physiology or vice versa, they are clearly coordinated in this system. From an evolutionary perspective, differences in germination phenology may result from different selective pressures for species of different physiologies. For example, individuals of high-WUE species may have experienced higher fitness when germinating from seeds that required less time for imbibition prior to germination, whereas the opposite pattern may have occurred in low-WUE species. Alternatively, all species may have had greater fitness when they germinated at different times because of reduced competition, and this may have resulted in disruptive selection favoring unique suites of physiological traits. This link between phenology and physiological traits clarifies the mechanisms by which species differ in their demographic responses to varying environmental conditions. Phenological differences allow species to use resources at different times, under different environmental conditions, which influences their survival and reproduction and may reduce competition for resources (Pavon and Briones, 2001; Fargione and Tilman, 2005).

Phenological and physiological differences can promote species coexistence by temporally partitioning resource use among species across a season (Schoener, 1974; Fargione and Tilman, 2005). In a prairie system, phenologically different species were more likely to coexist than those that had similar phenology because of the temporal dynamics of soil nitrate availability (Fargione and Tilman, 2005). In desert systems such as ours, where water is the primary limiting resource, phenological differences in growth activity temporally segregate water use among species with large differences in growth form, such as grasses versus shrubs (Went, 1948; Kemp, 1983). Differences in reproductive phenology are typically thought to promote coexistence by preventing competition for pollinator services (Stiles, 1977; Waser, 1978; Zimmerman, 1980; Osada et al., 2003). However, the production of flowers and fruits is known to be influenced by resource availability (Widen, 1991; Sandring et al., 2007), and this may be more important than pollinator availability in our desert system, where water is limiting and the species pool includes many predominantly selfing species.

Phenology and climate—High-WUE species tended to germinate earlier than low-WUE species in any given year. We have shown elsewhere that the high-WUE species have increased in abundance over time and have paradoxically germinated

later and under cooler conditions than the low-WUE species when averaged over the last 25 yr (Fig. 2B; Kimball et al., 2010). How can our results in the present study be reconciled with this previous observation? Over the period of our long-term study, the Sonoran Desert has experienced increased winter temperatures and decreased precipitation (McAfee and Russell, 2008). Germination-triggering rains have been arriving later in the season and now tend to occur in December rather than in October, which was common in the 1980s (Kimball et al., 2010). The unexpected result is that all plants have been germinating under colder temperatures, and high-WUE, demographically buffered species that photosynthesize well under low temperatures have increased in abundance (Fig. 2B). Thus, although species with high WUE germinate earlier in any given year, the gradual shift over the years to later, cooler germination and the progressive increase in abundance of high-WUE species has overridden this within-year pattern. Thus, on average, over the 25-yr study period, the high-WUE species have germinated later in the calendar year and under cooler conditions (Kimball et al., 2010).

Phenology and habitat—The open habitat between shrubs has greater temperature extremes and is drier than the under-shrub habitat (Appendix S4; Pake and Venable 1995). We do

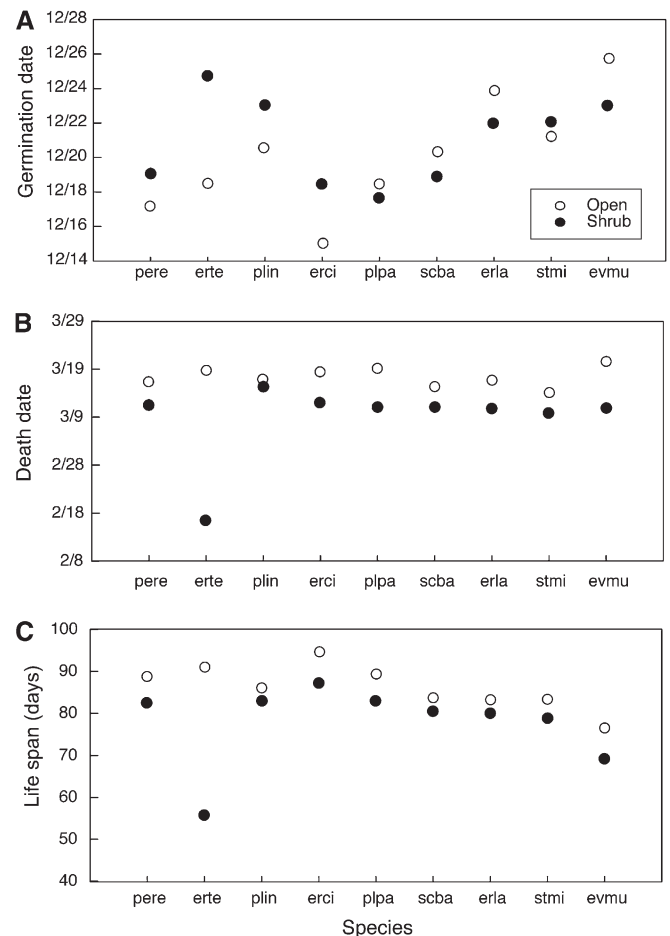


Fig. 4. Phenology of the nine focal species in the open and under shrubs from 1991 to 2009. (A) Average germination date. (B) Average death date. (C) Average life span.

not yet understand why timing of life cycle events differed in these two habitats, but the differences may reflect germination and/or growth physiology responding to temperature, moisture, and light differences. Low-WUE, demographically variable species germinate later in the season and have lower germination fractions, which suggests that they may require longer wetting to germinate. Soil water potential is known to influence germination (Evans and Etherington, 1990; Pritchard, 1991), so it is possible that increased moisture under shrubs may trigger germination earlier for these species than the drier soil in the open. Differences in the timing of reproduction and of the life span of some species in open compared with under-shrub habitats may be a result of differences in temperature or light optima that allow some species to have higher growth rates in one habitat than in the other. Soil water availability differs under shrubs and in the open because of differences in the interception of rainfall by foliage, evaporation from the soil surface, and uptake by roots at depth (Loik et al., 2004). In our system, the soil moisture data indicate that reduced bare-soil evaporation from under shrubs seems to be the most important factor influencing seasonal soil moisture dynamics (Appendix S4).

Conclusion—Phenological differences in Sonoran Desert winter annuals may explain how physiological traits promote differences in rates of germination, survival, and reproduction. The timing of precipitation changes from year to year, so species with different phenologies are favored in different years. The ability of high-WUE, demographically buffered species to grow and reproduce early in the growing season is likely attributable to their ability to photosynthesize at low temperatures. By contrast, the low-WUE, demographically variable species have phenologies that expose them to warmer conditions, resulting in high growth and reproduction when warm and wet, but high mortality when warm and dry. Our results illustrate how phenology, especially timing of germination and reproduction, is related to the physiological traits that are known to underlie species differences in population dynamics.

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