The contribution of germination functional traits to population dynamics of a desert plant community

Zhenying Huang,[1] Shuangshuang Liu,[2] Kent J. Bradford,[2] Travis E. Huxman,[3] and D. Lawrence Venable[4,5]

[1]*State Key Laboratory of Vegetation and Environmental Change, Institute of Botany, Chinese Academy of Sciences, Beijing 100093, China*
[2]*Department of Plant Sciences, University of California, Davis, California 95616, USA*
[3]*Department of Ecology and Evolutionary Biology, University of California, Irvine, California 92697, USA*
[4]*Department of Ecology and Evolutionary Biology, University of Arizona, Tucson, Arizona 85721, USA*

Abstract. Early life-cycle events play critical roles in determining the population and community dynamics of plants. The ecology of seeds and their germination patterns can determine range limits, adaptation to environmental variation, species diversity, and community responses to climate change. Understanding the adaptive consequences and environmental filtering of such functional traits will allow us to explain and predict ecological dynamics. Here we quantify key functional aspects of germination physiology and relate them to an existing functional ecology framework to explain long-term population dynamics for 13 species of desert annuals near Tucson, Arizona, USA. Our goal was to assess the extent to which germination functional biology contributes to long-term population processes in nature. Some of the species differences in base, optimum, and maximum temperatures for germination, thermal times to germination, and base water potentials for germination were strongly related to 20-yr mean germination fractions, 25-yr average germination dates, seed size, and long-term demographic variation. Comparisons of germination fraction, survival, and fecundity vs. yearly changes in population size found significant roles for all three factors, although in varying proportions for different species. Relationships between species' germination physiologies and relative germination fractions varied across years, with fast-germinating species being favored in years with warm temperatures during rainfall events in the germination season. Species with low germination fractions and high demographic variance have low integrated water-use efficiency, higher vegetative growth rates, and smaller, slower-germinating seeds. We have identified and quantified a number of functional traits associated with germination biology that play critical roles in ecological population dynamics.

Key words: community population dynamics; desert annuals; functional traits; germination; long-term research; population dynamics; population-based threshold model; Sonoran Desert; syndromes; trade-offs; Tumamoc Hill, Tucson, Arizona, USA.

Introduction

Ecologists face the challenge of determining how functional traits of organisms mediate the responses to the environment that determine population and community dynamics. Understanding such mechanisms is critical to building the predictive ecology that will help us to understand how populations and communities will respond to environmental change in the future. Early life events such as germination and plant establishment have been identified as important in determining population and community properties, along with other traits such as growth rates, stress tolerance, and flowering times (Grubb 1977, Geber and Eckhart 2005, Bader et al. 2009, Donohue et al. 2010, Wilczek et al. 2010, Stanton-Geddes et al. 2012,

Burghardt et al. 2015). In particular, seed germination has been shown to significantly influence plant life cycles and fitness (Baskin and Baskin 1984, Donohue et al. 2010, Burghardt et al. 2015), niche construction (Donohue et al. 2005), species coexistence (Angert et al. 2009), and community composition in response to climate change (Kimball et al. 2010). However, it remains unknown how germination functional traits (e.g., temperature and water potential thresholds, speed of germination, uniformity, etc.) contribute to long-term population processes of a community.

This paper explores the power of germination functional traits to predict population dynamics for a community of desert annuals near Tucson, Arizona, USA. Our results not only elucidate the relationship between the physiology of germination timing and long-term population dynamics of a community of coexisting plants, but also provide information and tools for predicting ecosystem responses to climate

change and for designing conservation strategies. This is the first paper to correlate germination traits with long-term population dynamics for a whole community, which can reveal syndromes and correlations that studies of single species cannot. Specifically, this paper addresses the following questions:

(1) Do germination functional traits predict population ecology measured in the field?
(2) How do germination traits determine which species germinate more or less than average in particular years, and how is this determined by the environment in those years?
(3) What germination traits, growth and physiological traits, and population ecology parameters tend to be associated with each other in this desert community?
(4) How much does germination contribute to population dynamics in comparison to the growth-phase processes of survival and reproduction?

Previous studies of this system have shown how the physiology of growth and water use contribute to the control of population and community dynamics. Early work examined relative growth rates and patterns of biomass allocation of the species in this community in relation to water-use efficiency and long-term demographic variation (Angert et al. 2007). Results showed how morphological and physiological traits influence demographic tracking of environmental variability and determine a community-wide trade-off between growth rate and water-use efficiency (Huxman et al. 2008). These results were extended to investigate functional trait contributions to species coexistence (Angert et al. 2009, 2010). Long-term shifts in community composition favored cold-adapted species in response to a multi-decadal trend of increasing temperature and decreasing rainfall (Kimball et al. 2010). This apparent paradox is explained by phenological differences among species and a multi-decadal shift to later-season germination at colder temperatures (Kimball et al. 2011). The relation of cold adaptation to water-use efficiency and growth rate was determined by analyzing the temperature responses of field-grown plants (Gremer et al. 2012, Barron-Gafford et al. 2013). Other studies showed how growth and water-use traits determine which species survive and reproduce more or less than average in particular years and how this is determined by the environment (Kimball et al. 2012). More recent studies have measured natural selection on growth and water-use traits in the wild (Kimball et al. 2013), genetic structure of growth and water-use traits (Angert et al. 2014), and how growth-phase physiology determines competitive outcomes in wet vs. dry conditions (Gremer et al. 2013). This system also has been central to the testing of adaptive bet-hedging theory (Pake and Venable 1996, Clauss and Venable 2000, Moriuchi et al. 2000, Venable 2007, Gremer

and Venable 2014). The present study fills an important gap by quantifying the contribution of germination functional traits to the dynamics of these variable populations.

MATERIALS AND METHODS

Study site

The study site is located at the Desert Laboratory at Tumamoc Hill, Tucson, Arizona, USA (32°13′N, 111°0′W, 723 m above sea level), on an alluvial plain dominated by *Larrea tridentata* (creosote bush) receiving about 300 mm of annual precipitation, on average (Bowers and Turner 1985). The Desert Laboratory is a nature preserve and field station that has been protected from grazing since 1906 (Venable 2007).

Demographic data

Sonoran Desert winter annuals germinate at this site with autumn and early winter rains, usually between October and January. Flowering occurs in spring, and plants complete their life cycles before the onset of the May–June arid fore-summer (Venable and Pake 1999, Clauss and Venable 2000, Venable and Kimball 2013). In 1982, permanent plots (initially 14, increased to 72 in 1990) were established along a 250-m transect located both in the open and under creosote shrub canopies. Germination (seedling emergence) is mapped following rains, and survival and reproduction are measured until all plants have died. Detailed demographic data are available for each species in the community for the past 32 yr, including germination date, germination fraction (of total seeds present; G), per capita survival to reproduction (l), average number of seeds produced by survivors (b), and lifetime per capita fecundity (lb, the product of the previous two parameters) (Venable and Kimball 2013).

Every year starting with the 1989/1990 season, the density of viable non-germinating seeds was estimated from soil cores. These annual samples were collected after all germination had occurred and before new seeds fell. The fraction of seeds that germinate in a particular year was determined from the density of seeds that germinated in the long-term plots and the density of seeds that did not germinate from the seed bank samples. In this paper, we consider both year-to-year variation as well as the 20-yr average (across years 1990–2009) in natural germination fractions. Average germination date for each species was calculated by using the date of the germination census (expressed as days since 1 October). When species had multiple germination cohorts in a year, average germination date was calculated as the average germination date of all seeds that germinated. We calculated the 25-yr average germination date for each species by averaging the mean germination dates for the 25 yr

(1983–2007). Mean seed mass of each species was measured in at least 2 yr and averaged. Demographic variation was calculated as the standard deviation of 30 yr of the natural log of *lb*, the per germinant fecundities.

The 13 common winter annual species used in this study (Appendix S2: Table S1) constitute 68% of all winter annual individuals that have germinated on the long-term plots during the last 30 yr. One of the species, *Pectocarya heterocarpa*, is amphicarpic, producing two types of aerial seeds (nutlets) as well as a third type of basal seed below ground. We refer to the two aerial seed types as "winged seeds" (nutlets with a margin covered with barbed, membranaceous wings) and "long seeds" (long, narrow nutlets with no wings). The basal seeds are larger, oblong, and without barbs.

Germination experiments

Freshly matured seeds were collected from 50–100 plants of each of the 13 study species in the spring of 2010. The seeds were shaken from the dry infructescences of each species and placed in paper bags for storage. Germination tests were conducted on fresh seeds while other seeds were tested following after-ripening for 4 or 5.5 months at constant 45°C, constant 30°C, and under natural field conditions (see Appendix S1 for storage details). Seed germination trials were carried out in petri dishes in growth chambers at different constant temperatures ranging from 8° to 35°C and water potentials ranging from 0 to −1.0 MPa in light (details are in Appendix S1).

A brief introduction to hydrothermal time models is provided in Appendix S1. Thermal time (θ_T) for suboptimal temperatures is calculated as the time from imbibition to completion of germination of an arbitrary percentage (t_g, where g is the germination percentage, e.g., 50%) multiplied by the degrees above a minimum or base temperature (T_b) permitting germination, i.e., $\theta_T(g) = (T - T_b) \, t_g$. The hydrotime requirement for germination (θ_H) is similarly the difference between the current environmental water potential (Ψ) and the minimum or base water potential required for germination (Ψ_b) multiplied by the time to completion of germination of a specific percentage (g) of the seed population (θ_H) = ($\Psi - \Psi_b(g)$) t_g. These variables were fitted using the germination data with calculation methods implemented in an Excel program written by S. Liu and K. J. Bradford (Gummerson 1986, Bradford 1990, 2005, Alvarado and Bradford 2002).

We determined base (T_b), optimal (T_o, where germination is most rapid) and ceiling (T_c) or maximum germination temperatures (Alvarado and Bradford 2002, Bradford 2002, Allen et al. 2007). Seed germination rates (the inverse of time to a specific percentage, $1/t_g$) increase linearly with temperature above T_b until the optimal temperature for germination is reached. Above the optimal temperature, the rate declines until

the T_c is reached for the germination fraction considered ($\theta_T = (T_c(g) - T) \, t_g$). Water potential requirements for germination are somewhat similar to those of temperature. Germination rates increase linearly as water potential increases above the base water potential for the germination fraction ($\Psi_b(g)$) (Gummerson 1986, Alvarado and Bradford 2002). Because water potentials cannot be higher than zero, the maximum germination rate is generally at $\Psi = 0$ MPa. To obtain the cardinal temperatures, only data from seeds germinated in pure deionized water (0 MPa) were used. Base temperature (T_b) and the mean and variance of ceiling temperatures (where $T_c(50\%)$ was used as the estimate for T_c) were estimated with probit regression of the cumulative germination fraction as a function of thermal time for suboptimal and supraoptimal temperatures at which seeds germinated in the experiment. Basal temperatures were constrained to be greater than or equal to 0°C because seeds do not germinate in frozen water. Optimal temperatures (T_o) were calculated as the intersection between the sub- and supraoptimal rates as a function of temperature:

$$T_o = (a_{supra} - a_{sub})/(b_{sub} - b_{supra})$$

where a_{supra} and b_{supra} are the intercept and the slope, respectively, from the supraoptimal regression equation, and a_{sub} and b_{sub} are the intercept and the slope for the suboptimal regression equation.

Functional traits utilized as predictors in the analyses of this paper include T_b, T_o, and T_c, thermal time to 50% germination ($\theta_T(50)$), base water potential ($\Psi_b(50)$) after 4 months of after-ripening, maximum percentage germination for fresh seeds, and maximum percentage germination after 4 months of after-ripening. The latter two traits were directly calculated from the raw germination data, whereas the others were fitted as described previously. Thermal time was log-transformed and maximum germination percentages of fresh and 4-months after-ripened seeds were arcsine square-root-transformed for statistical analyses.

Analyses

To determine how germination functional biology predicts field population biology (question 1), we used hierarchical partitioning analysis to determine the relative importance of each functional predictor to each ecological dependent variable (Chevan and Sutherland 1991, Murray and Conner 2009). The ecological dependent variables were 20-yr average germination fraction, germination date, seed size, and long-term demographic variance. Hierarchical partitioning analysis is a robust way to determine the independent effects that a set of collinear predictors have on a dependent variable. The first step is to remove predictor variables that are not correlated with the dependent variable (i.e., having "zero-order"

correlation coefficients near zero). This filtering of zero-order correlations close to zero has been shown to be the best way to detect and remove spurious correlations. The importance of each remaining predictor is then calculated as its average contribution to the model R^2 across all possible models. This method of averaging the effect of each predictor over all possible regression models (comparing all models including and excluding each predictor) provides a more robust assessment of the relative importance of each predictor (the independent effect) than any single regression model. This is because it partitions the variance shared by correlated predictors into the variance contributed by each effect independently while controlling for multicollinearity. This technique has been shown to recover the true structure of simulated data better than partial correlations, semipartial correlations, standardized regression coefficients, and Akaike weights (Murray and Conner 2009). The independent effect is essentially the proportion of the variance in Y independently explained by a predictor. The independent percentages for all variables in the model add up to 100% and are thus useful to compare predictors on a common ratio scale. To interpret the results of hierarchical partitioning analysis, we primarily focus on the independent effects and independent percentages, but also report R^2 and P values from univariate linear regressions. Species are the unit of observation, so residual degrees of freedom are all near but less than 13. Hierarchical partitioning as described by Chevan and Sutherland (1991) was conducted using SAS 9.3 with the hierarchical partitioning macro written by K. M. Berger and M. M. Conner (*personal communication*) based on a Dominance Analysis macro written by R. Azen and R. Ceurvorst.

To investigate the consequences of functional traits for germination fraction in specific years in response to weather variation (question 2), we reduced germination physiology to a single summary variable. Then we examined the relationship of germination physiology to greater or less than average germination of the different species across years. First, the traits, base water potential, $\Psi_b(50)$; thermal time, $\theta_T(50)$; and ceiling germination temperature, $T_c(50)$ were reduced to a single principal component axis. This first principal component explained 75% of the variation in the data and described among-species variation in terms of fast vs. slow germination speed. High values of the principal component are correlated with high (less negative) base water potential, high thermal time, and low ceiling germination temperature, i.e., traits associated with slow germination speed. We then expressed individual-year field germination fractions as deviations from the long-term (20-yr) species averages. This germination deviation then was plotted against the principal component of germination physiology to elucidate which germination physiologies had higher or lower than average germination in a particular year. A negative slope means that fast germinators had higher germination in relation to their long-term average than did slow germinators in that year. A positive slope indicates the opposite: slow germinators had higher germination in relation to their long-term average relative to fast germinators. We plotted the slopes through time to show variation among years in how different physiologies germinated more or less under natural conditions. The intercept (centered at the average principal component score) of these regressions indicates whether desert annuals in general germinated more or less than average in particular years. We then correlated the slopes and intercepts with weather variables that might discriminate between fast and slow germinators or promote germination generally. The yearly weather variables tested were the average temperature on days with rain during the October–January germination season, average temperature early in the germination season (October–November), date of first germination, the number of rainfall events that triggered germination that year, total precipitation associated with all germination cohorts for the year, the amount of rain associated with the first germination cohort, maximum and median germination season rainfall event (October–January), and the average October–January southern oscillation (El Niño) index.

To examine trait correlations and trade-offs broadly across the life history (question 3), we conducted a principal component analysis on germination functional traits (median base water potentials and thermal times), the various field ecological variables already mentioned (demographic variance, germination fraction, germination date, and seed mass), and growth functional traits (stomatal conductance, integrated water-use efficiency, and a principal component score representing the traits underlying a trade-off between relative growth rate and water-use efficiency). Details of how the different traits were measured are given in *Methods: Demographic data* and in the Supplemental Material, but some aspects that could cause confusion are explained here. Average survival is the 31-yr species average (1983–2013) of survival from germination to reproduction. Average seed set is the 31-yr species average (1983–2013) of the seed set of plants that survived to reproduction (ln-transformed for this analysis). Integrated water-use efficiency, Δ (based on $\delta^{13}C$ ratios calculated following Farquhar et al. (1989) as $\Delta = (\delta a - \delta p)/(1 + \delta p/1000)$, where δa is the carbon isotope ratio of CO_2 in the atmosphere [assumed to be -8‰] and δp is the measured carbon isotope ratio of the leaf tissue), has lower (positive) values as water-use efficiency increases. In this analysis, we call it "water-use efficiency" and reverse its sign so that higher values mean higher water-use efficiency, as intuition would suggest. The variable called "growth physiology" is a principal component score from a previous analysis. It is constructed from five key traits that underlie the growth capacity–low-resource tolerance trade-off: leaf:mass

ratio (the ratio of leaf dry mass to total dry mass), maximum electron transport capacity, specific leaf area (the ratio of leaf area to leaf dry mass), relative growth plasticity, and leaf nitrogen content (details given in Angert et al. 2009). Higher values of this principal component indicate traits underlying lower relative growth rate and higher water-use efficiency. Thus, we conducted a principal component analysis on a broad range of traits, one of which, growth physiology, is itself coded by principal component scores from a previous principal component analyses on more specific growth and resource use-efficiency traits. The previously described principal component analysis on germination traits used to investigate the consequences of functional traits for germination fraction in specific years was not used in this broad analysis of traits.

To determine the importance of germination for the population dynamics of each species (question 4), we compared germination fraction, survival, and fecundity as predictors of year-to-year changes in population size using hierarchical partitioning analysis. Population size each year was determined as the number of seeds just prior to initiation of germination, estimated as the number of seeds germinating per square meter plus the number of seeds per square meter that did not germinate. Because annual plants may be absent above ground for much of the year or even skip germination in some years, it is important to consider both seeds and seedlings to measure true population size. The increase from year y to year $y + 1$ was calculated as the log ratio of the two years' population sizes. A value of 1 was added to each population size to avoid taking the log of zero. The predictors were the arcsine square root of germination fraction, survival from germination to reproduction, and the log of mean fecundity of survivors.

RESULTS

Germination and hydrothermal time parameters

Growth chamber experiments revealed a wide array of germination behaviors and functional traits for the species in this winter annual guild. Some species such as *Draba cuneifolia*, *Evax multicaulis*, and *Schismus barbatus* were almost completely dormant when fresh and only gradually lost dormancy with after-ripening (Appendix S2: Fig. S1). Other species such as *Plantago* spp., *Pectocarya* ssp., and *Stylocline micropoides* germinated only at the lowest temperatures when fresh, but gradually broadened their temperature range for germination to include higher temperatures as after-ripening progressed. Most species germinated to high percentages by 4 months of after-ripening for at least some temperatures and after-ripening regimes. However, two species, *Eucrypta micrantha* and *Vulpia octoflora*, germinated little even after 5.5 months of after-ripening. *Vulpia octoflora* had maximum germination of around

40%, whereas *Eucrypta micrantha* germinated less than 20% under all conditions (Appendix S2: Fig. S1). Although base temperatures for germination did not vary much among species (0–3.7°C), the optimum temperatures varied from 8.6° to 27.6°C and ceiling temperatures for germination varied from 15.3° to 50.9°C among species (Appendix S2: Table S2). Thermal times to 50% germination (11–141 h) and base water potentials (−2.32 to −0.19 MPa) also varied greatly among species, reflecting a gradient of slow to fast germination following imbibition. The variation in base water potentials among seeds in the germinating populations (i.e., the uniformity of response among individual seeds) also differed among species, as indicated by standard deviation values of $\sigma = 0.19$–0.79 MPa (Appendix S2: Table S2). The base water potential with associated standard deviation reported in Table B2 is the lowest base water potential chosen from among all the temperature and after-ripening treatments. The temperature and after-ripening treatment that resulted in the lowest base water potential is also given in Table S2.

These germination functional traits were not all independent of one another and their pattern of correlation is revealing as to how germination functional traits interact to control the rate and percentage of germination (Appendix S2: Table S3). Species with high thermal time to 50% germination (i.e., it takes them a long time to germinate following imbibition) tend to have a low maximum germination of fresh seeds, a low maximum germination of 4 months after-ripened seeds, a high base water potential (requiring high water content of the soil for germination), and a high standard deviation of base water potential (greater variation in germination time). In principle, seeds could take a long time to germinate and require high water potential to germinate, but still all germinate at once after the appropriate thresholds are reached. Yet they do not: slow-germinating species that require high water potential to germinate also have high variation in germination time (Appendix S2: Table S3).

Variation in germination fraction due to differences in species responses to weather variation

First we used both univariate regression and hierarchical partitioning analysis to assess how functional germination traits were related to population ecology traits measured on each species (question 1). We found that the 20-yr average field germination fraction was best explained by base water potential for germination, ceiling germination temperature, and thermal time to germination, with higher field germination fractions associated with lower base water potentials, higher ceiling temperatures, and shorter thermal times (Table 1).

The hierarchical partitioning analysis showed that species germinating later in the season in natural

TABLE 1. Relative importance of germination functional traits as predictors of ecological traits of desert annual species near Tucson, Arizona, USA; 20-yr (1990–2009) mean field germination fractions, 25-yr (1982–2007) mean field germination dates, seed size, and 30-yr demographic variance are dependent variables.

Ecological trait and functional predictors	$R2$	Sign	P	Independent effect	Independent percentage
20-yr mean field germination fractions					
Base water potential	0.4466	−	0.02	0.1926	36.30
Ceiling temperature	0.3952	+	0.03	0.1824	34.40
Thermal time	0.3451	−	0.05	0.1558	29.40
25-yr mean field germination date					
Thermal time	0.3346	+	0.04	0.1773	34.40
Optimal temperature	0.2673	−	0.07	0.1694	32.80
Maximum germination (4 month AR)	0.3238	−	0.04	0.1173	22.70
Base water potential	0.1727	+	0.15	0.0518	10.00
Seed size					
Thermal time	0.4008	−	0.01	0.2208	34.10
Base water potential	0.3171	−	0.03	0.1295	20.00
Maximum germination (4 month AR)	0.1039	+	0.24	0.1223	18.90
Maximum germination (fresh)	0.3011	+	0.04	0.121	18.70
Ceiling temperature	0.1472	+	0.15	0.0544	8.40
30-yr demographic variance					
Thermal time	0.7267	+	0.0004	0.2707	28.90
Maximum germination (fresh)	0.6318	−	0.002	0.2328	24.90
Base water potential	0.4921	+	0.01	0.1366	14.60
Maximum germination (4 month AR)	0.31	−	0.06	0.1164	12.50
Base temperature	0.2619	−	0. 09	0.0896	9.60
Ceiling temperature	0.274	−	0.08	0.089	9.50

Notes: The first three columns give results from univariate linear regressions, including the coefficient of determination (R^2), the sign of the relationship, and P values for the regression coefficients. The final two columns give the results of a hierarchical partitioning analysis that quantifies the independent effect of variables after accounting for correlations between variables (see *Analyses*). The independent percentage is the percentage of the variance explained by each variable relative to the others (sums to 100%). Germination after 4 months of after-ripening is abbreviated as "4 month AR."

populations had longer thermal times to germination, lower optimal temperatures for germination, lower maximum germination percentages of 4-months after-ripened seeds, and higher base water potentials (Table 1). This makes sense because it is hotter early in the fall-to-winter germination season, so higher temperature optima permit earlier germination. Also, high thermal time, low germination at 4 months of after-ripening, and high base water potential are all found in species with slow, and hence in this case, late germination.

Larger-seeded species had shorter thermal times to germination, lower base water potentials, higher germination percentages after 4 months of after-ripening, higher germination percentages of fresh seeds, and higher ceiling germination temperatures (Table 1). These are all indicators of fast germination, demonstrating that in this guild of desert annuals, large-seeded species germinate faster than small-seeded species.

Species with higher demographic variance of germinated seeds (standard deviation of ln-transformed fecundity per germinant) had longer thermal times to germination, lower germination percentages of fresh seeds, higher base water potentials, low germination of 4-months after-ripened seeds, and lower base and ceiling germination temperatures (Table 1). These are all traits associated with slower, later germination and low germination fractions. Thus, species with more variable fitness of germinated seeds tend to have cautious, delayed germination strategies.

In summary, thermal time to germination and base water potential were the germination functional traits most consistently and strongly related to aspects of natural population dynamics. Their relationships to ecological variables were parallel: variables positively associated with thermal time were positively related to base water potential. This is to be expected, as changes

in base water potential affect the speed of germination across temperatures, with higher (more positive) base water potentials resulting in longer thermal times to germination (Alvarado and Bradford 2002).

Germination traits, population dynamics, and correlations with environmental factors

We also investigated whether germination traits determine which species germinate more or less than average in particular years (question 2). When the slopes of the regressions of germination deviations from long-term average against germination physiology PC score are plotted against time, we can see how different germination physiologies do better or worse than average in different years (Fig. 1A). In some years, such as 1993, 2003, and 2005, fast germinators germinated more relative to their long-term average than did slow germinators. In other years, such as 2006 and 2009, slow germinators germinated more relative to their long-term average than did fast germinators. These shifting slopes illustrate how the species × year interaction for germination fraction relates to germination physiology. In some years, such as 1992, 2001, and 2012, almost all species germinated more than average (high centered intercept) and germination physiology did not have a big effect (shallow slope; Fig. 1B). In other years, such as 2002 and 2006, all species germinated less than average.

This variation in germination as a function of germination physiology probably is due to environmental differences among years. We searched for the relationships between the germination vs. physiology slope and weather differences among years and found the strongest correlation to be with the temperature during rainfall ($R^2 = 0.44$, $P < 0.004$). High temperature during rainfall result in greater germination of species with fast-germination physiologies in that year. Thus, fast-germinating species are likely to germinate in years with early autumn/winter rain before the cool season or in years when it was relatively warm during rainfall events, regardless of when they occurred in the germination season. Other variables had $R^2 < 0.2$ and were mostly nonsignificant. The intercept, which reflects the tendency of all species to germinate more in a given year, was strongly negatively related to the average temperature for October and November ($R^2 = 0.46$, $P < 0.0005$) and positively related to the total precipitation associated with all germination cohorts for the year ($R^2 = 0.60$, $P < 0.0003$). Thus, as might be expected in a desert environment, this guild of annuals tends to have higher germination in years with cool autumns and high precipitation during the germination season. Other weather variables were not significant.

Trait syndromes and ecological strategies

To look for syndromes of traits and ecologies that go together (question 3), we conducted a principal
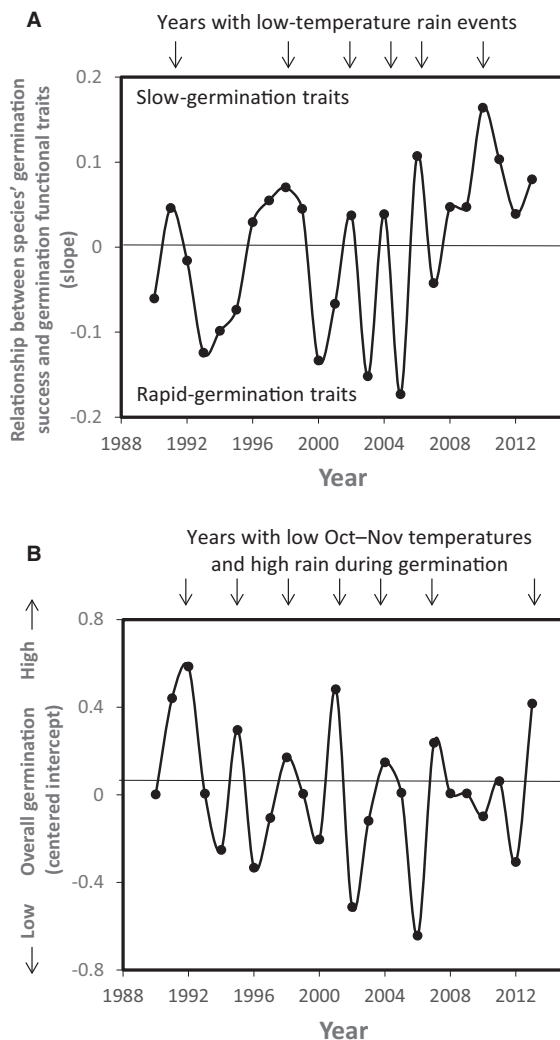

FIG. 1. (A) Slopes and (B) intercepts of the regressions of the deviation of each year's germination fraction for a given species from that species' long-term average as a function of the species' principal component score from an analysis of the three most important germination functional traits for germination fraction. The regression was conducted separately for each year with species used as data points. Negative slope indicates that, in the year in question, species with fast-germination traits had a higher germination fraction relative to their long-term average than did species with slow-germination traits. Slopes tended to be more negative in years with higher temperature when rains occurred during the germination time period. The centered intercept (intercept at the x-axis average) indicates high vs. low germination fraction years. Overall germination tended to be higher in years with more total precipitation during the germination season and lower mean temperatures during October and November.

component analysis on the ecological variables from long-term field data, the most important germination functional traits, and important growth-phase functional traits that we have previously researched extensively (Angert et al. 2007, 2009, Huxman et al. 2008). The first principal component captures 61% of the variance in the original 11 variables. It shows

that species with high demographic variation and low field germination fractions have small seeds, low average seedling–adult survival, high average seed production of plants that survived to reproduce, low integrated water-use efficiency, high relative growth rate (low "growth physiology" score), and germination physiology suggestive of slow germination (Table 2). Interestingly, a score summarizing species position on a growth rate–water-use efficiency trade-off (growth physiology) is highly correlated with germination thermal time, base water potential, and seed size, such that fast-germinating species tend to have large seeds, high post-germination water-use efficiency, and slow growth rates (Table 2).

Importance of germination fraction for changes in population size

The relative importance of germination, survival, and reproduction to changes in population size varied from species to species (question 4). Germination was most important for five species, survival for five species, and fecundity for three species (Appendix S2: Table S4). All three factors contributed significantly to population change in seven of the 13 species.

DISCUSSION

Combining long-term data with comparative physiological ecology can yield a deeper understanding of

TABLE 2. Principal component analysis of germination and growth physiology along with various field ecological measurements.

Variable	PCR 1 correlations
Stomatal conductance	0.349
Water-use efficiency	−0.728
Growth physiology	−0.875
Thermal time, ln-transformed	0.827
Base water potential	0.809
Germination date	0.279
Seed mass, ln-transformed	−0.974
Average survival	−0.622
Average seed set, ln-transformed	0.951
Germination fraction	−0.949
Demographic variance	0.867

Notes: Values reported are the correlations between the species variables and the scores for the species on the first principal component. Water-use efficiency (WUE) is based on Δ but the sign is reversed so that high values mean greater water-use efficiency. Growth physiology is the PC score from a different principal components analysis of variables underlying a vegetative growth rate–water-use efficiency trade-off and a high value of "growth physiology" means traits favoring high WUE but low relative growth rate (see *Methods* for details on these and other variables here).

the contribution of functional traits to population and community dynamics and can focus our attempts to understand the evolution of plant physiological characteristics (Medina et al. 1984, Mooney 1991). In previous studies, we have examined how growth and water use can affect population and community ecology (Angert et al. 2009, Kimball et al. 2012, Huxman et al. 2013). Those studies shed light on trait evolution, responses to climate change, differential response to competition, and the forces that shape coexistence among species. Here we have extended this to include germination physiology and have discovered some important linkages. Species differences in thermal times to germination, base water potentials for germination, and variously base, optimum, or maximum temperatures for germination under controlled temperature and water conditions, were strongly related to the 20-year mean germination fraction in nature, the average germination date, seed size, and long-term demographic variation. These patterns relating growth-chamber physiological measurements to population parameters in natural field conditions make intuitive sense.

Higher germination fractions in nature are found for species with hydrothermal traits favoring fast germination: short thermal time and low base water potential. Also, high maximum temperature for germination allows a species to start germinating earlier in the fall season, resulting in more germination opportunities and thus higher cumulative germination fractions. Germination fraction is a population property with important implications for evolutionary bet-hedging and species coexistence in this community (Angert et al. 2009, Gremer and Venable 2014).

Similarly, species that have higher temperature optima, short thermal times, and low base water potentials tend to germinate earlier in the season. Germination date has important ecological implications. In this community, hydrothermal traits associated with germination later during the season result in cooler temperatures for seedling establishment and growth. This can be beneficial with regard to seedling water stress if species have appropriately adjusted temperature optima for growth, which seems to be the case for these species (Kimball et al. 2011, Barron-Gafford et al. 2013, Gremer et al. 2013). However, later-germinating species have less time to grow and may experience asymmetric competition with earlier-germinating species (Kelly and Levin 1997, Verdu and Traveset 2005).

We found that larger-seeded species germinated faster, had lower thermal times and base water potentials, and had higher maximum temperatures for germination. Germination rates in relation to seed size have previously been investigated at both intra- and interspecific levels (Baskin and Baskin 2014). Most studies have found that larger seeds germinate faster (Weis 1982, Tripathi and Khan 1990, Prinzie

and Chmielewski 1994, Greipsson and Davy 1995, Simons and Johnston 2000, Du and Huang 2008). Some studies report that smaller seeds germinate faster or to higher percentages (Stamp 1990, Zhang 1993), whereas in other species, germination is not affected by seed size (Cideciyan and Malloch 1982). Some studies suggest that larger seeds should germinate more quickly to escape seed predators attracted to their larger resource package (Alcantara and Rey 2003, Gomez 2004). Greater resource reserves also may improve the chances of seedling establishment, making germination less risky and perhaps favoring faster, less cautious germination (Venable and Brown 1988). Some authors suggest that larger seeds have more protein and carbohydrate reserves that allow them to germinate more readily (Tripathi and Khan 1990, Seiwa 2000, Du and Huang 2008). Reports of smaller seeds germinating faster or no relationship between seed size and germination rate suggest that although the pattern we found of larger seeds germinating faster is the most common, it is not universal, apparently varying with the ecological and evolutionary forces, such as fire or predation, operating in a particular environment.

Species having high year-to-year variance in seed production per germinant had small seeds and hydrothermal traits associated with slow and, hence, fractional germination. This is predicted by life-history theory about bet-hedging. Species experiencing greater variance in the fitness of germinants are expected to have low germination fractions (Ellner 1985*a*, *b*, Gremer and Venable 2014).

Community ecologists are interested in species differences, but they are also interested in variation in species differences. For example, the species × year interaction for germination fraction is an important component of the storage effect mechanism for species coexistence in this community (Angert et al. 2009). Here we found a link between species × year interaction for germination and species differences in germination physiology. Fast-germinating species germinated more in years with relatively warm rain events, whereas slow-germinating species germinated more with cool events. Angert et al. (2009) showed that species × year interactions for per germinant fecundity also contribute to the storage effect and are related to species differences in growth and water-use physiology. Kimball et al. (2010) extended this by showing how specific aspects of weather favored different growth physiologies in different years.

Ecologists have long used the related concepts of trade-offs and syndromes as organizing principles, from the *r*–*K* gradient of MacArthur and Wilson (1967) and the CSR triangle of Grime (1977) to the macroecological trade-offs of functional traits (Wright et al. 2004). Today it is widely thought that many of the functional constraints that underlie trade-offs and shape life histories also affect interspecific

interactions, mechanisms of coexistence, and community structure (Grubb 1977, Chesson and Huntly 1988, Tilman and Pacala 1993, Venable et al. 1993, Bazzaz 1996, Turnbull et al. 1999, Rees et al. 2001). In our desert winter annual system, we have previously identified a trade-off between growth rate and water-use efficiency that has important implications for community structure and dynamics (Angert et al. 2009). There is also a relationship between germination fraction and year-to-year temporal variance in the fitness of germinants (Venable 2007, Gremer and Venable 2014). Here we expand and synthesize these analyses to show that low-germination, high-demographic-variance species are also low-integrated-water-use efficiency, high-growth-rate species and have smaller seeds (Fig. 2). These small-seeded, high-growth-rate species tend to have low survival from germination to reproduction but produce a large number of seeds if they survive. They may be highly successful under favorable conditions, but may perform very poorly under drought conditions due to their low water-use efficiency (Huxman et al. 2008). This high year-to-year fitness variance for the germinated plants probably constitutes the risk factor selecting for low germination fraction (Gremer and Venable 2014). Low germination fraction is associated with germination functional traits: high thermal time to germinate and high base water potential for germination. Low germination fraction is apparently more tenable ecologically for species in this community with small seeds that are better at avoiding seed predation, a potent evolutionary force in warm deserts. The relationships among these functional, population, and community factors are summarized in Fig. 2.

Collectively, these analyses demonstrate that germination biology has important impacts on plant population dynamics. We previously compared the relative importance of variation in germination, survival, and fecundity for year-to-year changes in population size, concluding that germination was the primary determinant in seven of nine species (Kimball et al. 2010). Here we revisit this question with more years of data on 13 species and a modified analytical approach. We found that germination was the most important factor for many species, but that survival and fecundity were the most important factors for others, and that for seven of 13 species, changes in population size were significantly related to all three factors. This new analysis comes to the more nuanced conclusion that germination plays a prominent role in population size changes in this community, along with survival and fecundity.

The reason for the difference in conclusions is that the Kimball et al. (2010) analysis used a slightly different calculation, describing population changes from year to year as ln(seedlings germinating in the previous year divided by seedlings germinating in the current year). This ignores ungerminated seeds in the soil, which, for
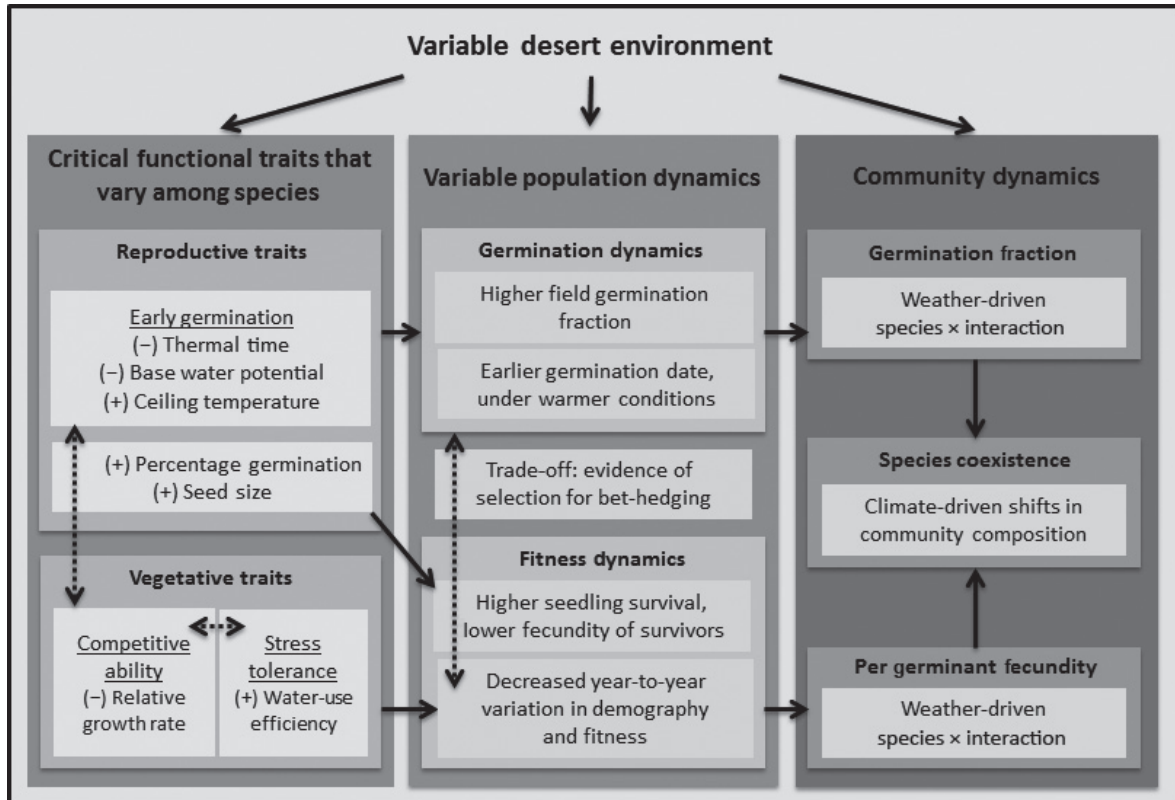
Fig. 2. Conceptual diagram of relationship of measured functional reproductive and vegetative traits to population and community dynamics, using a hypothetical rapid- germination, high water-use efficiency species as an example. Trade-offs are indicated with double-headed connectors with dashed lines; links between processes at different scales are connected with arrows; the nature of contributions to components are indicated by (+) and (−).

desert annuals, can be the entire population in a year of insufficient rainfall for germination. To better capture the size of the entire population, here we estimated population size as the density of seeds germinating plus the density of seeds that did not germinate.

The conclusions of our study probably are not restricted to the highly variable desert environment. A previous study with *Arabidopsis thaliana* on intraspecific variation has shown that seed dormancy, vegetative growth rate, and flowering time vary along a latitudinal gradient and that their covariation changes with latitude (Debieu et al. 2013). A variety of other studies (but not all) have shown potentially adaptive correlations between germination traits and usually early post-germination traits (Donohue et al. 2010, Donohue 2014, Burghardt et al. 2015). For example, germination niches with respect to temperature, light, water availability, or ion concentration often have corresponding seedling establishment niches (Donohue et al. 2010). However, it is rare to synthesize community covariation patterns for such a broad array of functional and population dynamic traits over several decades, which has permitted us to uncover the complex ecological syndromes that structure this desert annual community.

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