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BRIEF COMMUNICATION

Population histories of variable reproductive success and low winter precipitation correlate with risk-averse seed germination in a mediterranean-climate winter annual

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Abstract

Premise: Seed germination involves risk; post-germination conditions might not allow survival and reproduction. Variable, stressful environments favor seeds with germination that avoids risk (e.g., germination in conditions predicting success), spreads risk (e.g., dormancy), or escapes risk (e.g., rapid germination). Germination studies often investigate trait correlations with climate features linked to variation in post-germination reproductive success. Rarely are long-term records of population reproductive success available.

Methods: Supported by demographic and climate monitoring, we analyzed germination in the California winter-annual *Clarkia xantiana* subsp. *xantiana*. Sowing seeds of 10 populations across controlled levels of water potential and temperature, we estimated temperature-specific base water potential for 20% germination, germination time weighted by water potential above base (hydrotime), and a dormancy index (frequency of viable, ungerminated seeds). Mixed-effects models analyzed responses to (1) temperature, (2) discrete variation in reproductive success (presence or absence of years with zero seed production by a population), and (3) climate covariates, mean winter precipitation and coefficient of variation (CV) of spring precipitation. For six populations, records enabled analysis with a continuous metric of variable reproduction, the CV of per-capita reproductive success.

Results: Populations with more variable reproductive success had higher base water potential and dormancy. Higher base water potential and faster germination occurred at warmer experimental temperatures and in seeds of populations with wetter winters.

Conclusions: Geographic variation in seed germination in this species suggests local adaptation to demographic risk and rainfall. High base water potential and dormancy may concentrate germination in years likely to allow reproduction, while spreading risk among years.

KEYWORDS

annual plants, base water potential, Clarkia xantiana, demography, hydrotime model, mediterranean climate, Onagraceae, precipitation, seed dormancy, seed germination

Seed germination behavior influences the post-germination environments that plants encounter and can determine where plant populations establish and persist. Understanding the factors responsible for the evolution of germination traits is therefore critical to understanding geographic distributions (Donohue et al., 2010), species segregation along environmental gradients (e.g., Silvertown et al., 2015), and responses to climate change (Walck et al., 2011).

Seed germination enables but does not guarantee new seed production. When and where the fitness costs of mistimed germination are high, germination traits are expected to evolve that reduce the risk of incurring those costs (Baskin and Baskin, 2014). For example, persistent seed dormancy and long seed lifespan, which can spread the risk of failure in time (bet-hedging), are expected to evolve in annuals when failure risk is sufficiently variable and unpredictable

(Cohen, 1966; Brown and Venable, 1986; Gremer and Venable, 2014; Finch-Savage and Footitt, 2017; ten Brink et al., 2020). If seeds are not in deep physiological or physical dormancy, then risk-aversion may arise from germination that is restricted to ranges of light, temperature, moisture, and other cues that correlate with low risk (Cohen, 1967; Baskin and Baskin, 2014; Gremer et al., 2016; Finch-Savage and Footitt, 2017; Duncan et al., 2019). In other words, germination in response to strict cues can reduce the chance that seeds germinate when or where conditions do not support establishment (Bewley et al., 2013; Baskin and Baskin, 2014; Lamont and Pausas, 2023). For example, in winter-wet, summer-dry mediterranean climates, germination requirements for low temperature and persistent soil moisture reduce the risk of germinating after rare summer rainfall events (Thanos et al., 1995; Carta et al., 2022). More generally, having high base water potential (i.e., the threshold soil water potential above which germination occurs at a given percentage; Bradford, 1990, 2018) may be a risk-reduction adaptation where seasonal rainfall in some years is insufficient for reproduction (Arène et al., 2017). Risk aversion also can apply to the speed of germination. Once seeds are stimulated to germinate, short delays between imbibition and germination may allow early seed production, reducing the risk of reproductive failure if adverse conditions arrive soon (Donohue et al., 2010). The above overview identifies three non-mutually exclusive forms of risk-averse seed germination: (1) delayed germination that spreads risk, (2) adaptive cuing that avoids risk, and (3) rapid germination after seeds receive predictive stimuli, which may allow seedlings to escape risk.

Among populations of the same species, one would expect the degree of risk-averse germination to correlate with year-to-year variation in per-capita reproductive success (Cohen, 1966; Brown and Venable, 1991; Arène et al., 2017; ten Brink et al., 2020). Years of complete reproductive failure (zero seed production) are expected to contribute disproportionately to selection for bet-hedging and adaptive germination cuing (Cohen, 1966, 1967). Studies of intraspecific variation in risk-averse germination usually are based on gradients in putative climate drivers (e.g., Philippi, 1993; Clauss and Venable, 2000; Torres-Martínez et al., 2017) rather than also using demographic records (but see Tielbörger et al., 2012; Liu et al., 2020). The most informative long-term demographic data would come from multiple population censuses per year, enabling estimates of among-year variation in per-capita reproductive success, directly relevant to evolutionary models of germination (e.g., Siegmund et al., 2023). Once-annual censuses at the seed-production stage, however, also can identify years of complete reproductive failure. Such failures would be expected to generate strong selection in favor of genotypes that avoided germinating in those years, causing rapid adaptive evolution (e.g., Metz et al., 2020; Kooyers et al., 2021; Benning et al., 2023). Therefore, it is worth considering whether (1) populations known to have highly variable per-capita reproductive success from year to year and (2) populations known to have experienced recent complete reproductive failures have evolved more risk-averse germination.

A recent study of the California winter annual *Clarkia xantiana* subsp. *xantiana* (Onagraceae) leveraged intensive long-term demographic monitoring to evaluate density-independent evolutionary models of bet-hedging (Siegmund et al., 2023). Although the models predict benefits to between-year dormancy in some populations, they do not accurately predict observed among-population variation in annual germination fraction (Siegmund et al., 2023). Unexplained variation may arise from other causes. For example, negative density dependence among seedlings can favor higher dormancy by reducing the benefits of germinating in otherwise favorable years (Kortessis and Chesson, 2019), and within-season environmental variation also can select for greater dormancy (ten Brink et al., 2020). It also is possible that adaptive variation in predictive germination (e.g., Gremer et al., 2016) occurs in *C. xantiana* subsp. *xantiana*.

Here we report the results of a laboratory study on intraspecific variation in germination in *C. xantiana* subsp. *xantiana*, including the possibility of adaptive variation in germination cuing. We collected seeds from 10 populations with known long-term variation in annual reproductive success. All 10 populations were censused at seed production, and a subset of six were censused twice annually, including one shortly after germination. We sowed seeds across a gradient of water potential and at three temperatures, estimating at each temperature two germination traits derived from the hydrotime model (Bradford, 1990): base water potential for 20% germination (Ψ_{b20}), and time to germination weighted by water potential above base (hydrotime, HT). We also estimated a dormancy index (DI) based on the percentage of viable but ungerminated seeds for each population at each temperature. With mixed-effects models that included a random block factor, we analyzed trait responses to (1) chamber temperature (3 levels), (2) discrete variation in population reproductive success (presence or absence of a complete reproductive failure in demographic records; 2 levels), and (3) continuous climate covariates (winter mean and spring CV of precipitation). The more detailed demographic data available for six populations enabled a complementary analysis that evaluated trait responses to a continuous metric of reproduction (the coefficient of variation of per-capita reproductive success) and to temperature. We predicted that (1) Ψ_{b20} and DI decline at lower, more winter-like temperatures (risk avoidance in a Mediterranean climate); (2) populations with histories of greater variation in reproductive success exhibit higher Ψ_{b20} (risk avoidance), higher DI (risk spreading), and shorter HT (risk escape); and (3) trait values associated with risk-aversion (high Ψ_{b20}, short HT, and high DI) correlate with low and/or variable precipitation.

MATERIALS AND METHODS

Study system

Clarkia xantiana subsp. xantiana A. Gray (Onagraceae) is a winter annual in grassland, pine–oak savanna, and chaparral openings in inland southern and central California, United States, mostly between 500 and 1600 m a.s.l. (Eckhart and Geber, 1999). Its seeds germinate in the winter rainy season, and plants flower in late spring and early summer, dispersing seeds passively as capsules dehisce during summer drought (Moore and Lewis, 1965; Eckhart and Geber, 1999). Seeds can survive several years in soil; annual germination fractions average 10–30% (Eckhart, et al., 2011; Siegmund et al., 2023). The water relations of seed germination are likely to be important in this species because winter and spring precipitation are key determinants of its geographic range limits (Eckhart et al., 2011) and variation in water availability leads to small-scale occupancy, density, and individual performance (Geber and Eckhart, 2005; Eckhart et al., 2010; Kramer et al., 2011, Eckhart et al., 2017). In multispecies Clarkia communities, seed germination is the most important vital rate determining species' occupancy among soil patches (James et al., 2020).

Seeds for the experiment (see below) came from 10 populations in the Kern River drainage of the southern Sierra Nevada (Table 1). A map of the region and population locations is in Appendix S1. The study area is on the unceded traditional lands of the Tubatulabal people (Harvey, 2019), who once foraged for wild *Clarkia* seeds (Voegelin and Wheeler, 1938). Most of the area is in the Sequoia National Forest.

Each population's seeds came from bulked collections from approximately five fruits from each of approximately 25 haphazardly chosen parent plants per population in June 2020. Seeds sat dry in the dark at room temperature for 3 mo, before dry, dark storage at 4°C for 8 mo, until the start of the experiment. Though these storage conditions do not closely mimic field conditions, using seeds of uniform age and storage conditions eliminated contributions of age or storage to among-population variation. Because the seeds were field-collected, we cannot separate possible effects of population-specific maternal environment on seed germination traits (Philippi, 1993; Lampei et al., 2017) from genetic variation among populations. It is worth noting that maternal-environment effects on other traits in this taxon appear negligible (Benning et al., 2023).

Annual demographic monitoring began in 2005 on discrete populations in this area, accompanied by climate monitoring via a network of automated weather stations (Eckhart et al., 2011; Siegmund et al., 2023; Appendix S2). Twenty populations (including 6 of the 10 here) have been censused annually in 2006-2023, both at germination and at fruiting, in 30 permanent 0.5-m^2 plots per population, plus additionally haphazardly located plots, with the number of plots scaled to population area (see Siegmund et al., 2023). An additional 14 populations (including the other 4 of the 10 here) were censused annually at the fruiting stage from 2006 to 2019, in haphazardly distributed plots whose numbers were scaled to total population area (in this study, from 0.2 to 4 ha). Of this study's 10 populations, four produced no seeds (i.e., experienced complete reproductive failure) at least once during this period, determined when extensive searching by multiple field workers found no fruiting plants in plots or elsewhere within mapped population boundaries. Reproductive failures in three of four populations happened in distinctly dry growing seasons (2012–2014), while a fourth failed in a year of average rainfall, 2016, when a wildland fire burned the site during flowering (Appendix S2). The three “drought-failed” populations may occupy locations at greater risk long-term of drought failure. In any case, they persisted only in the seed bank in years of failure and therefore would be expected to have experienced selection for risk-averse germination. The

TABLE 1 Reproductive-success variation, seasonal precipitation, and elevation for each study population (Pop) of *Clarkia xantiana* subsp. *xantiana*. Abbreviations are as follows: RF is the absence (0) or occurrence (1) of a year of zero seed production, 2006–2020. CVRS is the coefficient of variation in per-capita reproductive success, 2006–2020. MWP and MSP are mean winter (November–January) and spring (February-June) precipitation, 2006–2023 (including years after seed collection, in the interest of using the longest climate record available). CVWP and CVSP are the coefficients of variation of winter and spring precipitation over that timespan, respectively.

Pop	RF	CVRS (%)	MWP (mm)	MSP (mm)	CVWP (%)	CVSP (%)	Elevation (m a.s.l.)
OSR	0	134	173	119	82	70	1060
GCN	0	137	137	96	78	73	860
S22	0	148	156	130	74	70	920
DEM	0	156	155	121	69	52	750
LCE	1	194	136	119	64	51	530
SM	1	215	141	106	77	71	1130
GL	1	N.A.	171	132	74	63	990
S63	1	N.A.	153	118	75	65	960
S8	0	N.A.	150	116	72	62	830
SRE	0	N.A.	158	108	81	68	945

N.A., not available

single fire event at the “fire-failed” population likely does not indicate greater risk of flowering-season fire there, but this reproductive failure would have similar evolutionary consequences as those by drought. In this way, we can assign to every population a discrete metric of variation in population reproductive success, “reproductive failure” (RF; Table 1; Appendix 2): no years of zero seed production ($N = 6$ populations) versus at least 1 year of zero seed production ($N = 4$) from 2005 to 2019 (Table 1). For the six study populations with more detailed demographic data that extended until the year of seed collection (2020), we were able to calculate a continuous measure of variation in reproductive success. This variable (CVRS; Table 1) we estimated as the coefficient of variation across years (2006–2020) of per-capita reproductive success: the product of seedling survival from germination to fruiting, mean fruit number, and mean number of seeds per fruit (Siegmund et al., 2023; M. A. Geber, D. A. Moeller, and V. M. Eckhart, unpublished data).

Experimental protocol

We used a growth-chamber experiment to determine seed-germination traits for each population (Figure 1). In each of two replicate blocks, we sowed seeds of each population at 12 water potentials (–0.33 to 0 MPa, in 0.03-MPa intervals) at three temperatures (5, 10, 15°C), scored seed germination at approximately 12-h intervals, and analyzed germination time courses to estimate population traits by the hydrotime model (Bradford, 1990). In this way, we determined three temperature-specific seed-germination traits related to ranges of water availability that stimulate germination, time to germination given those conditions, and seed dormancy. The 12 levels of water potential we chose simply to create a sensitive “instrument” to measure Ψ_{b20} and HT (i.e., a wide range and substantial number of levels of the independent variable, for more accurate linear regression-based estimates; see below). Deionized water was the 0 MPa solution. We made 33 custom solutions by adding polyethylene glycol (PEG 8000, Sigma-Aldrich, St. Louis, MO, USA), adjusting concentrations to match assigned water potentials at each experimental temperature (Michel, 1983; Bradford, 1990; Castillo-Lorenzo et al., 2019; López et al., 2021). Winter temperatures in the air and in shallow soil in this region are in the range of the lower two experimental levels, 15°C being more typical of fall or spring (Appendix S3). Pilot experiments indicated that these and nearby populations have zero or near-zero germination at temperatures above 20°C (V. Eckhart, B. Larson, and K. Tomczyk, Grinnell College, unpublished data).

Observational units for each treatment combination were sets of 100 seeds inside 10 by 10 cm Petri dishes (Figure 2). To assemble each dish, we placed in it two sterile cotton balls topped with a 75 mm square of germination blotting paper with 100 indentations (Seedburo Equipment Co., Des Plaines, IL, USA) and added 25 mL of solution. Then we placed 10 seeds from each of the 10 populations into the grid of indentations. After sealing the plate with Parafilm (Bemis, Neehah, Wisconsin, USA), we placed it and similar plates for the 11 other water potentials into one of three temperature chambers with broad-spectrum LEDs set on a 12-h cycle (Figure 1). Approximately every 12-h for 14 d, we counted seeds with emergent radicles. A 12-h light cycle (which applies at the equinoxes) represented a neutral intermediate between winter or summer day length. It also

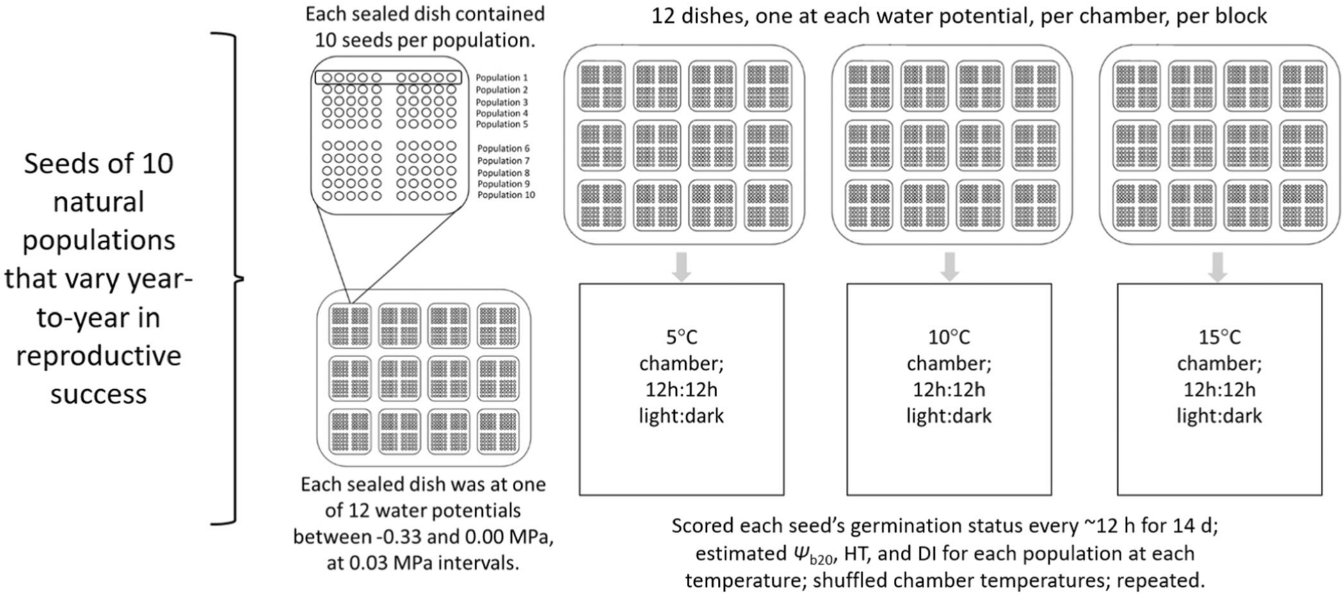

FIGURE 1 Outline of the protocol for estimating three seed-germination traits for 10 populations of *Clarkia xantiana* subsp. *xantiana*, at each of three temperatures.

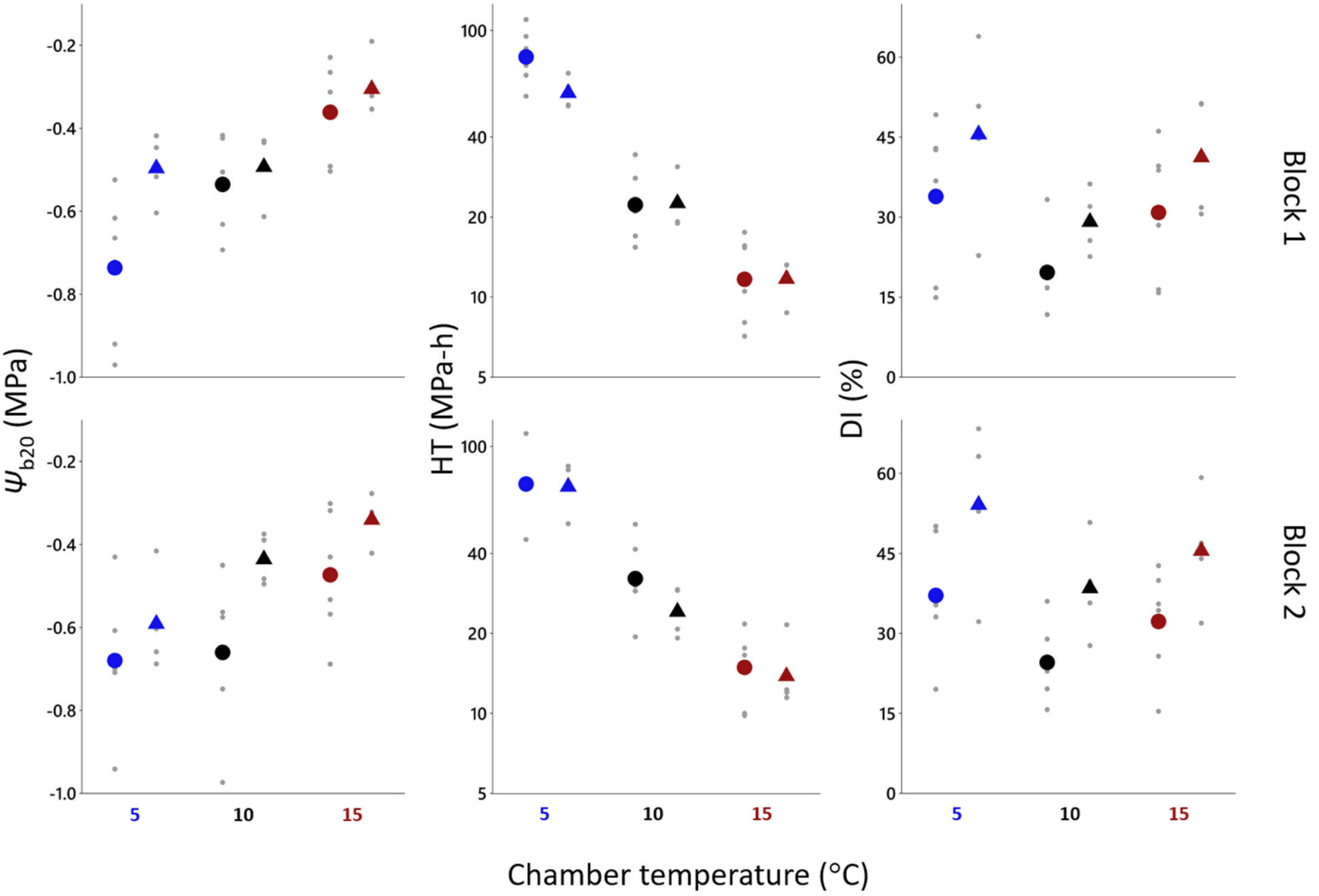

FIGURE 2 Seed-germination traits at three color-coded chamber temperatures for *C. xantiana* subsp. *xantiana* populations that did not ($N = 6$) or did ($N = 4$) experience a complete reproductive failure between 2006 and 2020. Large, color-coded symbols are means (circles for populations that did not experience a reproductive failure, triangles for those that did). Small gray circles are population values. Traits appear in columns. Top row is block 1. Bottom row is block 2.

had practical value, enabling us to score germination at approximately 12-h intervals while the chamber lights were on, without interrupting seeds' experience of "night." After each census, we shifted the position of each plate in its chamber. After 14 d, we tested the viability of ungerminated seeds by squeezing them with forceps to force embryos from seed coats and examine them (Baskin and Baskin, 2014). Assaying viability by examining embryos is as accurate or more accurate than doing so by tetrazolium staining (Frischie et al., 2020). Seeds lacking intact embryos totaled less than 3%. Between replicate blocks, we shuffled chamber's set temperatures. Thus, we followed the fates of 7200 seeds (10 populations, 10 seeds per population per dish, 12 water potential levels, 3 temperatures, 2 blocks). In one block, the –0.33 MPa, 15°C dish was upset, spilling seeds out of their assigned indentations before 14 d, any effects becoming part of the between-block variance.

Monitoring the accumulation of germinating seeds over time allows the estimation of parameters that describe a population's seed-germination water relations (the hydrotime model; Bradford, 1990, 2018), chiefly: the base water potential in MPa above which specified percentages of seeds germinate; and HT, the time to germination after experiencing water potentials above the base, weighted by the difference between water potential experienced and the base water potential (units are MPa-h). The customary percentage for base water potential is 50% (Bradford, 1990). We used 20% (Ψ_{b20}) because germination rates were too low in some experimental treatments to estimate base water potential for 50% germination and because *C. xantiana* subsp. *xantiana* annual germination fractions in nature average near 20% (Siegmund, et al., 2023). Linear regressions of the inverse of time to 20% germination against water potential estimated model parameters; the *x*-intercept of the regression line is Ψ_{b20}, and the inverse of this line's slope is HT (Appendix S4). We also estimated for each population a dormancy index, DI, the percentage of ungerminated, viable seeds that remained after 14 d, across all water potentials within a temperature treatment. Although DI is not a direct measure of between-year dormancy, it should correlate with the probability that seeds in a population remain in the seed bank.

Statistical analyses

Because our design included a random factor (block) and was unbalanced ($N = 6$ vs. $N = 4$ for the binary classification of RF), we used mixed-effects models to analyze trait variation (Bolker et al., 2009). We log-transformed HT to make its distribution approximately normal. The other traits did not require transformation.

For the full set of 10 populations, we fit the data to a mixed-effects model with block (2 levels) as a random factor, temperature (T: 5, 10, or 15°C) and reproductive failure (RF: 0 or 1) as fixed factors (including their interaction), and two covariates (Table 1): mean winter precipitation (MWP) and coefficient of variation of spring precipitation (CVSP). We selected these covariates to attempt to detect possible effects of average seasonal rainfall and variability in seasonal rainfall on germination traits, low mean and high variability being expected to increase risk. For the sake of teasing apart the effects of these variables, it was helpful that MWP and CVSP estimate mean and variation, respectively, but they have little correlation with each other ($r = 0.13$; $P = 0.72$). If low and/or variable precipitation is the main driver of reproductive failure and therefore risk-averse germination, then this analysis may detect effects of climate variables only. Alternatively, if failure status reflects unmeasured but important environmental variation or if recent failures caused the evolution of increased risk aversion, then we may also detect effects of population failure history.

For the subset of six populations with more demographic detail, we carried out a similar analysis to assess the influence of the continuous metric of reproductive success variation, CVRS. The mixed-effects model here included block as a random factor, temperature as a fixed factor, and CVRS as a covariate. Because this analysis is on a subset—rather than an independent set—of populations, it should be interpreted only as complementary.

We ran mixed-effects models and carried out other data analyses in Minitab version 21 (Minitab, State College, PA, USA). For mixed-effects models, variances were estimated by restricted maximum likelihood, with fixed effects' degrees of freedom determined by the Satterthwaite method (Appendix S5).

RESULTS

The analysis of 10 populations in which we considered discrete variation in reproductive success revealed that all germination traits varied with chamber temperature and with average winter precipitation at populations' home sites. Base water potential and dormancy also differed significantly in the expected directions, according to populations' reproductive-failure histories. Block effects were negligible (Appendix S5). A 5°C increase in chamber temperature ($F_{2,51} = 22.05$; $P < 0.0001$) and a history of reproductive failure ($F_{1,51} = 9.05$; $P = 0.003$) each increased Ψ_{b20} by approximately 0.1 MPa (Figure 2A; Table 2). With every 10-mm increase in mean winter precipitation, Ψ_{b20} increased by 0.04 MPa ($F_{1,51} = 9.77$, $P = 0.003$; Table 2). Each 5°C rise in chamber temperature reduced HT by about half ($F_{2,51} = 192.13$; $P < 0.0001$; Figure 2B; Table 2), and HT increased with mean winter precipitation ($F_{1,51} = 5.94$, $P = 0.018$; Table 2). At 10°C, DI was lower by 10–15% than at the other temperatures ($F_{2,51} = 9.95$; $P = 0.004$; Figure 2C; Table 2). A history of reproductive failure increased DI by over 10%, in absolute terms, across temperatures ($F_{1,51} = 14.71$, $P < 0.0001$; Figure 2C; Table 2). Each 10-mm increase in MWP reduced DI by about 3% ($F_{1,51} = 8.93$; $P = 0.004$; Table 2). There was no evidence of interactive effects of temperature and reproductive failure on any trait, nor did CVSP appear to influence any trait (Table 2).

Findings were similar in the six-population analysis with a continuous metric of variation in reproductive success. There were significant chamber-temperature effects, as above ($\Psi_{b20:}$ $F_{2,32} = 8.87$; $P = 0.001$; log HT: $F_{2,32} = 103.48$; $P < 0.0001$; DI: $F_{1,31} = 8.63$; $P = 0.004$). As with discrete variation, continuous variation in year-to-year reproductive success predicted higher base water potential and dormancy but did not influence log HT. With every 10% increase in the CVRS, Ψ_{b20} increased by 0.023 ± 0.008 MPa ($F_{1,32} = 8.48$; $P = 0.001$) and DI increased by 3.1 ± 0.5% ($F_{1,31} = 31.92$; $P = 0.001$).

TABLE 2 Mixed-model analysis of germination traits in 10 populations of *Clarkia xantiana* subsp. *xantiana* populations. Models had block (2 levels) as a random factor, temperature (T: 5, 10, or 15°C) and reproductive failure (RF: 0 or 1) as fixed factors, and covariates mean winter precipitation (MWP) and coefficient of variation of spring precipitation (CVSP). Significant predictors are bolded.

Trait	Source	Coefficient ± SE	$F_{[df,df]}$	*P*
Ψ_{b20}	**T**		**$22.05_{[2,51]}$**	**<0.0001**
	RF		**$9.75_{[1,51]}$**	**0.003**
	T × RF		$0.40_{[2,51]}$	0.672
	MWP	**−0.041 ± 0.013**	**$9.77_{[1,51]}$**	**0.003**
	CVSP	−0.003 ± 0.002	$1.39_{[1,51]}$	0.244
logHT	**T**		**$192.13_{[2,51]}$**	**<0.0001**
	RF		$0.76_{[1,51]}$	0.387
	T × RF		$0.31_{[2,51]}$	0.738
	MWP	**0.032 ± 0.013**	**$5.94_{[1,51]}$**	**0.018**
	CVSP	0.021 ± 0.020	$0.93_{[1,51]}$	0.338
DI	**T**		**$9.95_{[2,51]}$**	**0.004**
	RF		**$14.71_{[1,51]}$**	**0.0003**
	T × RF		$0.10_{[2,51]}$	0.903
	MWP	**−3.38 ± 1.13**	**$8.93_{[1,51]}$**	**0.004**
	CVSP	−0.52 ± 0.19	$0.08_{[1,51]}$	0.783

DISCUSSION

Populations of *C. xantiana* subsp. *xantiana* with greater year-to-year variation in reproductive success and lower average winter precipitation have evolved more risk-averse seed germination. This rare study, able to address whether climate and demography matter to seed-germination traits, discovered that both factors do, for two of three traits. High base water potential may have evolved as a risk-avoidance mechanism, and greater dormancy might have evolved to spread risk. Hydrotime is shorter in populations from more arid sites but appears to be independent of demography. The patterns of variation we discovered represent intraspecific niche variation (Holt, 2009), which we suspect expands the study species' geographic range by contributing to local adaptation. Moreover, the spatial variation in germination traits that has evolved suggests possible temporal trajectories of populations in response to climate change.

Two patterns were either shared by all populations, without interactive effects of demographic variation, or were sensitive to climate but not to demography. The increase in Ψ_{b20} with temperature suggests a mechanism that restricts germination to cool seasons (more likely to have sustained precipitation, therefore less risky), common in mediterranean-climate species (Thanos et al., 1995; Carta et al., 2022). Finding shorter HT in more winter-arid populations suggests potential escape from early-onset water deficits in those locations, but only if shorter HT enables earlier maturity.

Counter to one of our predictions, DI was lowest (i.e., germination fraction was highest) at the intermediate temperature, 10°C. Because of the experiment's limited time window and HT's overall decline with temperature, one would expect this measure of dormancy to be higher at the lowest temperature rather than the intermediate one. Instead, the pattern suggests that the optimal germination temperature is closer to 10°C than to 5°C. The decline in total germination at warmer (more summer-like) temperatures resembles findings in mediterranean-climate plants elsewhere, as noted above.

Because they discovered high evolutionary lability of base water potential, Arène et al. (2017) predicted that this trait may differentiate among populations of single species along precipitation gradients. Our findings are consistent with that prediction. Similarly, accessions of wild and cultivated annual *Brassica* from more arid areas had higher base water potential (Castillo-Lorenzo et al., 2019). Such patterns are not universal. Köchy and Tielbörger (2007) found no within- or among-species correlations between mean annual rainfall and base water potential (estimated by a simpler procedure) in 36 species from the eastern Mediterranean. López et al. (2021) found similar base water potentials in populations of a perennial bunchgrass along a precipitation gradient. Among species within locations, base water potential and related germination traits do not all converge on shared values, though there can be clusters of species within communities with risk-averse germination (Venable, 2007; Hu et al., 2015; Duncan et al., 2019; Liu et al., 2020; Bertuzzi et al., 2022). Nevertheless, the present findings indicate that populations within a species can become differentiated in base water potential. To the extent this trait can evolve rapidly (Arène et al., 2017), it may facilitate adaptation and persistence of plant populations where precipitation patterns also are changing rapidly as climate changes (Harp and Horton, 2022, 2023). Our findings of trait variation in space suggest that populations of *C. xantiana* subsp. *xantiana* in regions becoming more arid may evolve higher base water potential, greater dormancy, and shorter hydrotime, with the opposite direction in places that become wetter. In California, precipitation totals from intense winter storm events are projected to increase substantially within three decades (Chen et al., 2023), changes in rainfall timing and amount that also may affect seed-germination evolution due to demographic variation as well as climate.

Plant adaptation to water stress may come from avoiding drought altogether, escaping drought before it arrives, or delaying or tolerating dehydration (Burnette and Eckhart, 2021; Welles and Funk, 2021). With respect to seed germination traits, it is plausible that drought avoidance in *C. xantiana* subsp. *xantiana* arises from germination stimulated by low temperatures (Thanos et al., 1995) and high soil water potential (Arène et al., 2017). High base water potential may not only enable predictive germination that avoids drought, but also may underlie variation in seed persistence and the risk-spreading it provides (Huang et al., 2016).

Among desert annuals in one location, species with more variable demography and lower field germination fractions had higher base water potentials (Huang et al., 2016). We have limited power to assess whether seed germination traits in the present study predict within-species variation in germination fraction, as we only had six populations with both lab germination traits and field germination fractions. Moreover, the most comprehensive field germination fraction data come from 2005 to 2009, early in the demographic monitoring, and before any observations of complete reproductive failure. For those six populations, the mean field germination fraction (Siegmund et al., 2023) correlates negatively with Ψ_{b20} at winter-like temperatures, 5°C (Spearman $r = -0.89$, 95% CI -0.99 to -0.07) and (nonsignificantly) at 10°C (Spearman $r = -0.66$, 95% CI -0.96 to 0.43). Thus, it is plausible but equivocal that the germination traits we measured explain some of the variation in field germination fraction. More comprehensive studies would be helpful (e.g., sampling more populations; targeting resurrection experiments before and after failures [Benning et al., 2023]; and scoring germination traits not measured here, such as stimulation by light and fluctuating temperatures, cues of shallow burial that would have similar seed-bank effects [Saatkamp et al., 2011]).

CONCLUSIONS

Geographic variation in seed germination in this species suggests local adaptation to demographic risk and rainfall. High base water potential and dormancy may concentrate germination in years likely to allow reproduction, while spreading risk among years. The spatial variation in germination traits that has evolved in this species suggests possible temporal trajectories of populations of this species and others in response to climate change, including the evolution of higher base water potential and greater dormancy where reproductive success becomes more variable among years, and of those trait values plus shorter hydrotime where germination seasons become more arid.

AUTHOR CONTRIBUTIONS

I.H.V. and V.M.E. conceived the investigation, with V.M.E. providing administration and resources. M.A.G., D.A.M., and V.M.E. conceived, collected, and administered the long-term demographic and climate data and acquired funding. I.H.V. devised methodology, carried out the investigation, began formal analysis, and wrote the original draft. V.M.E. extended formal analysis, made new visualizations with I.H.V., and led writing at the review and editing stages, with the assistance of all other authors.

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OPEN RESEARCH BADGES

This article has earned an Open Data badge for making publicly available the digitally-shareable data necessary to reproduce the reported results. The data are available at https://doi.org/10.17632/tskwf63npx.2.

DATA AVAILABILITY STATEMENT

Data are available at Mendeley Data as doi:10.17632/tskwf63npx.1.

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SUPPORTING INFORMATION

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

Appendix S1. Map of the *Clarkia xantiana* subsp. *xantiana* study region and population locations.

Appendix S2. Timespans of the collection of demographic and climate data, plus occurrences of complete population reproductive failure in *Clarkia xantiana* subsp. *xantiana* populations, 2006–2023.

Appendix S3. Sources, methods, and patterns in climate data for a study of germination traits in 10 populations of *Clarkia xantiana* subsp. *xantiana*.

Appendix S4. Regression analyses for estimating base water potential and hydrotime of *Clarkia xantiana* subsp. *xantiana* seeds of 10 populations at three growth-chamber temperatures and in two blocks.

Appendix S5. Random-effects tests and other details of mixed-effects models of the responses of three seed germination traits to experimental temperature and to populations' climate covariates and discrete or continuous variation in reproductive success.

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