

ARTICLE

Geographic variation in offspring size: Long- and short-term climate affect mean seed mass of *Streptanthus* populations

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Abstract

Offspring size is a key functional trait that can affect subsequent life history stages; in many species, it exhibits both local adaptation and phenotypic plasticity. Variation among populations in offspring size may be explained by various factors, including local climatic conditions. However, geographic variation in climate may be partitioned into long-term and interannual sources of variation, which may differ in their effects on population mean offspring size. To assess environmental correlates of offspring size, we evaluated geographic variation in seed mass among 88 populations representing 6 species of *Streptanthus* (Brassicaceae) distributed across a broad climatic gradient in California. We examined the effects of temperature-mediated growing season length and precipitation on population mean seed mass to determine whether it is best explained by (1) long-term mean climatic conditions; (2) interannual climate anomalies (i.e., deviations in climate from long-term means) during the year of seed development, or (3) interactions between climate variables. Both long-term mean climate and climate anomalies in the year of collection were associated with population mean seed mass, but their effects differed in direction and magnitude. Relatively large seeds were produced at chronically wet sites but also during drier-than-average years. This contrast indicates that these associations may be generated by different mechanisms (i.e., adaptive evolution vs. phenotypic plasticity) and may be evidence of countergradient plasticity in seed mass. In addition, populations occurring in locations characterized by relatively long growing seasons produced comparatively large seeds, particularly among chronically dry sites. This study highlights the need to consider that the responses of seed mass to long-term versus recent climatic conditions may differ and that climate variables may interact to predict seed mass. Such considerations are especially important when using these patterns to forecast the long- and short-term responses of seed mass to climate change. The results presented here also contribute to our broader understanding of how climate drives long-term (e.g., local adaptation) and short-term (e.g., phenotypic plasticity) variation in functional traits, such as offspring size across landscapes.

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KEYWORDS

California, climate anomalies, climate change, countergradient plasticity, functional trait, geographic variation, life history, local adaptation, offspring size, phenotypic plasticity, *Streptanthus*

INTRODUCTION

Examining the relationship between local environmental conditions and phenotype has a long history in evolutionary ecology as a means to infer the outcome of natural selection on functional traits, such as offspring size, which affects subsequent life history stages in many species (Allen, 1877; Baker, 1972; Clausen et al., 1948; Koski & Ashman, 2015; Marshall et al., 2018; Sakata et al., 2017). Variation in offspring size across environmental gradients may reflect an optimization of maternal investment per offspring via natural selection in response to chronic climatic conditions (Marshall et al., 2018; Pettersen et al., 2019). However, short-term, annual deviations in climate (e.g., warmer- or cooler-than-average years), which are experienced by most populations, may also influence maternal investment and, in turn, offspring size from year to year. Thus, geographic variation in offspring size among populations may be generated by responses to both short-term climate anomalies and long-term mean, chronic climatic conditions, two potentially independent components of variation in local environmental conditions. Few studies of any traits have aimed to detect, measure, and interpret their independent effects on population mean phenotype (Anderson et al., 2012; Ensing & Eckert, 2019; Mazer et al., 2020; Ramírez-Valiente et al., 2009), yet these two sources of variation in environmental conditions may have qualitatively different effects on phenotype, and associations may reflect distinct processes (e.g., adaptation vs. plasticity). Studies disentangling the effects of long- versus short-term variation in climate on key functional traits can help us to identify the conditions under which phenotypes respond to climate variation, to predict the direction and mechanism of these responses, and to identify the eco-evolutionary consequences of such responses for subsequent life history stages (Etterson, Schneider, et al., 2016; Fricke et al., 2019; Heilmeyer, 2019). Here, we use geographic variation in seed mass to demonstrate that the effects of short-term climate anomalies on offspring size can be isolated from the effects of long-term mean, spatial variation in climate. We analyze variation in seed mass, but the approach taken is broadly applicable to any system for which data on population trait values and climate are available.

The size of individual offspring, such as seeds, affects subsequent life history stages because larger offspring

often have greater resource reserves and resource-acquiring capacities than smaller offspring (Marshall et al., 2018). In plants, phenotypic variation in seed mass can affect germination timing, dispersal distance, demography, and, ultimately, population- and community-level dynamics (Fricke et al., 2019; Leishman et al., 2000; Moles & Westoby, 2003; Walck et al., 2011). Extrinsic factors, including local climatic conditions (Konarzewski et al., 2012; Murray et al., 2004), edaphic conditions (Simpson et al., 2017), the intensity of competition (Larios et al., 2014; Moles et al., 2007), and the presence of seed predators (Gómez, 2004), as well as intrinsic factors, such as a tradeoffs between seed size and number (Smith & Fretwell, 1974) and mating system (Mazer et al., 2020; Tateyama et al., 2021), may influence a population's optimum seed mass, contributing to the evolution of variation in seed mass among populations and species. To date, research on the adaptive significance of seed mass within species has focused primarily on how long-term mean, local climatic conditions can influence a population's optimum seed size (Konarzewski et al., 2012; Lázaro & Traveset, 2009; Murray et al., 2004; Wang et al., 2019).

Several studies have demonstrated associations between seed mass and long-term mean (i.e., chronic) climatic conditions, suggesting that chronic conditions may generate genetically based variation in population mean seed mass within or among species (Crouch & Vander Kloet, 1980; De Frenne et al., 2010; Konarzewski et al., 2012; Mazer et al., 2020; Murray et al., 2004). Among populations and species, seed mass has been associated with long-term mean precipitation (i.e., chronically wet vs. arid locations); however, the direction of the relationship differs among studies. The production of large seeds has been associated with arid locations (Azcárate et al., 2010; Baker, 1972; Konarzewski et al., 2012; Murray et al., 2004), as well as with more mesic sites (Harel et al., 2011; Liu et al., 2013; Moles et al., 2007; Qiu et al., 2010), depending on taxon. The long-term mean length of the temperature-mediated growing season (often estimated as cumulative growing-degree days [GDD]), during which seeds develop and mature, may also impose selection on seed mass (Crouch & Vander Kloet, 1980; de Frenne et al., 2010; Galen & Stanton, 1993; Li et al., 1998). For example, the so-called developmental window hypothesis proposes that selection may favor smaller seeds in climates with short growing seasons in order to ensure that seeds can complete development before environmental conditions deteriorate (Baker, 1972; Daws et al., 2004;

de Frenne et al., 2010; Marshall et al., 2018). These studies have helped to detect the environmental conditions that may drive seed mass evolution; however, none were designed to determine whether the effects on mean seed mass of long-term climatic conditions and of year-specific deviations from such conditions differ in magnitude or direction (but see Mazer et al. [2020]).

The mean seed mass of a population or taxon may respond differently to chronic or long-term mean climatic conditions than to short-term deviations from long-term mean climatic conditions experienced by most populations from year to year. For example, populations in chronically hot and dry environments may produce relatively large seeds, supporting the hypothesis that large seeds represent an adaptation to arid environments (Baker, 1972; Konarzewski et al., 2012; Murray et al., 2004). However, during a hotter- or drier-than-average year, these same populations may produce relatively small seeds, representing a plastic response to limited water resources under unusually harsh growing conditions (Mazer et al., 2020). Few studies have investigated whether traits respond differently to long-term versus short-term, interannual climatic conditions (Anderson et al., 2012; Bontrager & Angert, 2016; Mazer et al., 2020; Ramírez-Valiente et al., 2009; Soper Gorden et al., 2016), yet the association between these two measures of local climate and seed mass may be generated by different mechanisms (i.e., local adaptation vs. phenotypic plasticity) (Bontrager & Angert, 2016; Mazer et al., 2020; Soper Gorden et al., 2016). Moreover, opposing responses of seed mass to long- versus short-term variation in climate may also suggest that plastic responses to climate differ in direction from adaptively generated clines (e.g., countergradient plasticity or nonadaptive plasticity) (Ensing & Eckert, 2019). Countergradient plasticity may hinder local adaptation and population persistence in novel environments, including future novel climatic conditions generated by climate change (Eckhart et al., 2004). Given that climate change is likely to increase the frequency of more extreme weather events, understanding how seed mass responds to short-term climate anomalies generated by such events versus how seed mass responds to long-term mean, chronic conditions (and assessing the relative direction of those responses) can help us predict whether populations or species will respond to climate change via evolutionary adaptation, phenotypic plasticity, or both (Davis et al., 2005; Dawson et al., 2011; Heilmeyer, 2019; Jump & Peñuelas, 2005).

Given that climate change is likely to affect many biologically important environmental variables including both growing season length (through increases in temperature) and precipitation, we need to gain a more complete understanding of how these climatic parameters—individually and in combination—affect mean seed mass

(Cayan et al., 2008; Crimmins & Crimmins, 2019; Polade et al., 2017). Few studies have assessed the importance of interactions between climatic parameters on seed mass (Larios et al., 2014; Soper Gorden et al., 2016), and despite the well-documented independent effects of both precipitation and growing season length on mean seed mass (Crouch & Vander Kloet, 1980; de Frenne et al., 2010; Konarzewski et al., 2012; Murray et al., 2004), to our knowledge, no studies have investigated how these variables interact to affect population mean seed mass. Understanding such interactions will improve our ability to predict how seed mass may respond to climate change.

With the goal of understanding the ecological and evolutionary drivers of seed mass variation among congeneric populations, we investigated the association between seed mass and both long- and short-term climate parameters among 88 populations (each sampled once between 1984 and 2018) representing 6 species of *Streptanthus* (Brassicaceae) distributed across a climatic gradient in California, an analytical approach similar to that used by Mazer et al. (2020). We addressed the following four questions: (1) Is geographic variation in population mean seed mass explained by variation among sites in long-term mean climatic conditions, local climate anomalies in the year of collection, or both? (2) Do long-term mean temperature-mediated growing season length (estimated by long-term mean accumulated GDD) and cumulative precipitation during fall, winter, and spring independently predict population mean seed mass? (3) Do cumulative precipitation and growing season length interact to affect geographic variation in population mean seed mass? (4) Do responses of seed mass to short- versus long-term mean precipitation and growing season length differ in magnitude or direction?

METHODS

Study system

Streptanthus (Brassicaceae) is a genus of annual, biennial, and short-lived perennial herbs that occur in the western United States (GBIF.org, 2019). *Streptanthus* occupies shallow gravelly or rocky soils with sparse vegetation, and many species in the genus are considered to be serpentine endemics (Cacho & Strauss, 2014; Safford et al., 2005). For this study, we sampled seeds from six species: *S. barbiger*, *S. breweri*, *S. glandulosus*, *S. hesperidis*, *S. polygaloides*, and *S. tortuosus*. These species occur in the California Floristic Province, and all experience a Mediterranean climate where precipitation

primarily occurs during cool winters and summers are generally warm and dry (Figure 1) (Love & Mazer, 2021). *S. barbiger* and *S. hesperidis* are narrowly distributed, rare species, whereas the remaining species are more broadly distributed. In California, *Streptanthus* populations begin to germinate in fall and winter, develop flower buds in late winter and early spring, and flower in spring or summer. All species used in this study are considered to be strictly annuals except for *S. tortuosus*, whose life history ranges from annual to short-lived perennial, depending on the population and local climatic conditions (Baldwin et al., 2012; Gremer, Chiono, et al., 2020; Gremer, Wilcox, et al., 2020). Seeds generally develop during spring and summer, depending on local growing conditions (Preston, 1991). Seeds do not have specialized structures such as awns or wings that facilitate long-distance dispersal, so seeds are dispersed locally and passively (Mayer & Soltis, 1994).

Seed collection and seed mass determination

Between 1984 and 2018, seeds were collected from a total of 88 populations of 6 species (2–40 populations/species; one sample/population per year) in the genus *Streptanthus*, with the aim of sampling each taxon across much of its geographic range. By sampling seeds from multiple species with various range sizes, we were able to capture a broader climatic gradient representing greater variation in both short- and long-term climatic conditions than if we sampled from a single species (Figure 1). Among 83 of these populations, seeds were collected from 6 to 66 maternal families per population ($\bar{x} = 24.2 \pm 11.5$ families) (Love & Mazer, 2021). The mean population seed mass for the remaining five populations was estimated from bulk collections (i.e., seeds from many individuals per population were collected and pooled). All seeds were stored in small, paper coin envelopes, placed inside sealed

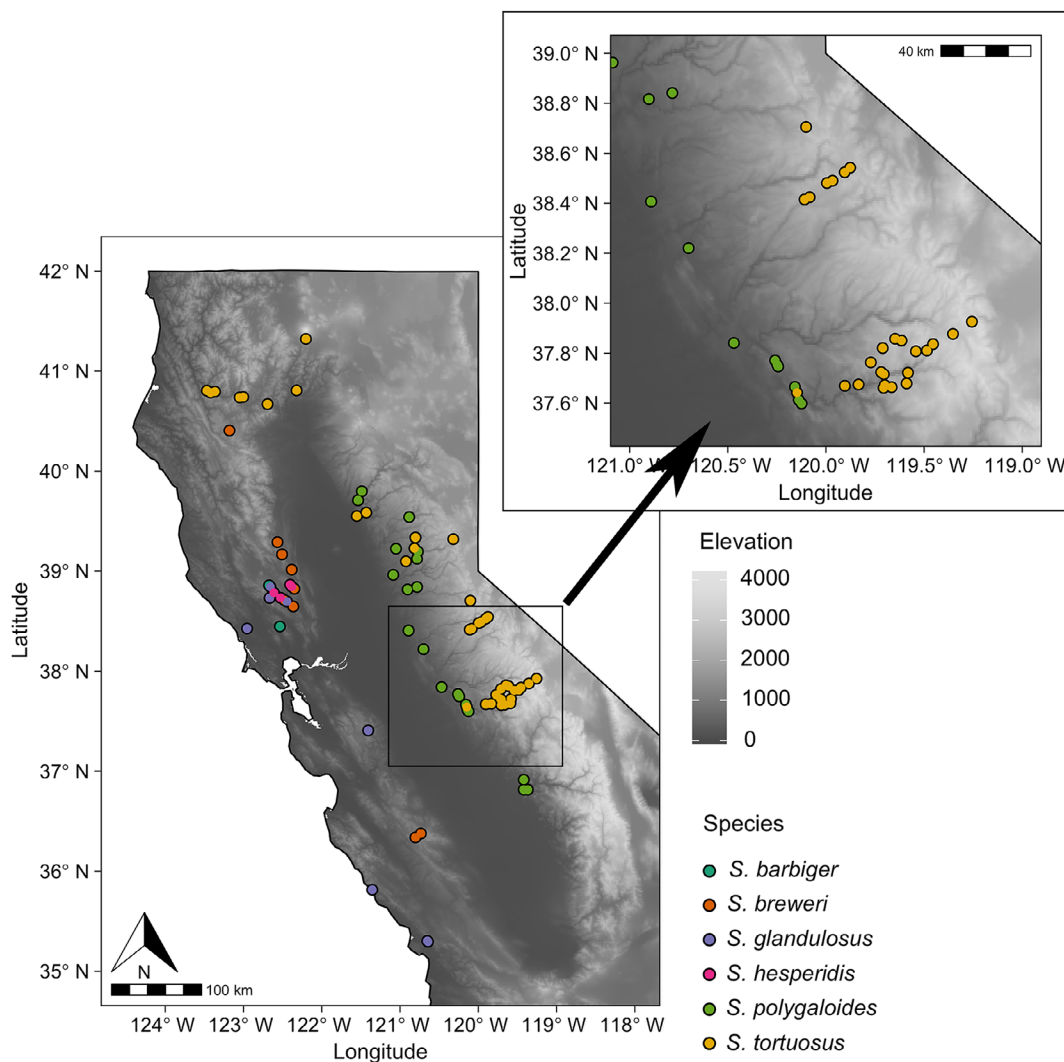


FIGURE 1 Locations of seed collection sites in California. Each point represents a population ($n = 88$)

plastic containers, and dehydrated with silica gel under refrigeration for at least 1 month prior to weighing.

To estimate the mean individual seed mass (MISM) per population, 35 seeds from each maternal family or bulk collection were weighed to the nearest 0.0001 g using a Cahn TA 4200 balance. The 35-seed weight was then converted to milligrams (mg) and divided by 35 to obtain a MISM for that maternal family or population (in the case of bulk collections). For populations represented by multiple maternal families, MISM was averaged among maternal families to obtain each population's MISM.

Climate data

To characterize the local climate during *Streptanthus*' growing season at each population's site, we used its GPS coordinates to extract the cumulative GDD above 5°C and the cumulative precipitation (PPT) (measured in millimeters) during winter, spring, and summer (WSS) from ClimateNA, a freely available climate database that provides locally downscaled historical climate values for a number of biologically relevant climate variables at any georeferenced location in North America (Hamann et al., 2013; Wang et al., 2016). For each site, the long-term mean climate parameters (30-year means, 1961–1990) and the climate parameters during the calendar year in which seeds developed and were collected were extracted from ClimateNA; these values were then used to calculate the climate anomaly (the deviation between the long-term climate mean for a given site and the conditions during the year of seed development) for each parameter (GDD and PPT) at each site. Years for which the site-specific anomaly for GDD (or PPT) was <0 were characterized by growing seasons (or cumulative precipitation) that were shorter (or drier) than the long-term mean value reported from 1961 to 1990.

Statistical analysis

To determine whether climate during the WSS growing season predicts seed mass among the sampled populations, two multiple linear regression models were designed to detect the effect of WSS GDD >5°C and PPT (in millimeters) on population MISM (Appendix S2). Both models included species as a main effect but differed in the combination of climatic variables included. The first model (Climate Model 1) included the effects of long-term mean WSS GDD and WSS PPT as well as their two-way interaction.

Climate Model 1 : Population MISM

$$= b_0 + b_1 \text{Species} + b_2 \text{WSS GDD}_{\text{long-term}} + b_3 \text{WSS PPT}_{\text{long-term}} + b_4 \text{WSS GDD}_{\text{long-term}} \times \text{WSS PPT}_{\text{long-term}} + \epsilon$$

The second model (Climate Model 2) was designed to detect the effects of local climate anomalies during the year of seed collection on population MISM independent of the long-term mean climate parameters. Model 2 includes the long-term climatic terms and the two-way interaction between them, as well as the WSS GDD and WSS PPT anomalies and the two-way interaction between them.

Climate Model 2 : Population MISM

$$= b_0 + b_1 \text{Species} + b_2 \text{WSS GDD}_{\text{long-term}} + b_3 \text{WSS PPT}_{\text{long-term}} + b_4 \text{WSS GDD}_{\text{long-term}} \times \text{WSS PPT}_{\text{long-term}} + b_5 \text{WSS GDD}_{\text{anomaly}} + b_6 \text{WSS PPT}_{\text{anomaly}} + b_7 \text{WSS GDD}_{\text{anomaly}} \times \text{WSS PPT}_{\text{anomaly}} + \epsilon$$

The output of these two models were then ranked by the Akaike information criterion (AIC), which balances model complexity with performance, to determine which model is best based on this criterion (Appendix S2) (Burnham et al., 2011). Both models were constructed using ordinary least squares (OLS) regression and significance testing was based on type III sums of squares using the *car* package and the *lm()* function in R (Fox & Weisberg, 2019). All predictor variables were mean centered to remove correlations between the main effects and their interactions (Schielzeth, 2010). Mean centering was performed using the *meanCenter* function in the *rockchalk* package (Johnson, 2019). To test for differences among species in their MISM, we calculated least-square means and conducted pairwise comparisons among all species using a Tukey adjustment in the *emmeans* package in R (Lenth, 2021). To aid with the interpretation of significant interactions, a Johnson–Neyman interval analysis was performed using the *interactions* package (Bauer & Curran, 2005; Long, 2019). The Johnson–Neyman interval analysis indicated the range of values of the moderator (e.g., WSS GDD) in which the slope of the predictor (e.g., WSS PPT) was significantly different from 0 at $\alpha = 0.95$. To test for collinearity among predictor variables, variance inflation factor (VIF) values and Pearson's correlation coefficients were calculated among all variables in Climate Models 1 and 2. All analyses were performed in R version 3.6.1 (R Core Team, 2020).

RESULTS

Correlations among climate variables

Pearson's correlation coefficients (r) among site-specific climate variables range from $|0.02|$ to $|0.53|$. The strongest correlation was between long-term mean WSS GDD and WSS PPT (-0.53 , $p < 0.001$, $n = 88$) (Appendix S1: Figure S1); sites that have relatively long growing seasons are also relatively dry. By contrast, the weakest correlation was between long-term mean WSS PPT and the WSS PPT anomalies during the year of seed development (-0.02 , $p = 0.87$) (Appendix S1: Figure S1); sites that experienced wetter-than-average years when the seeds were collected were no more likely to be chronically relatively wet or chronically relatively dry. The VIF values among variables in Models 1 and 2 were less than 3. The values of both r and VIF indicate low levels of collinearity among the variables included as main effects (Zuur et al., 2010).

Model selection and seed mass variation among species

Both climate models produced similar results (Appendix S2); however, Climate Model 2, which included all predictors, produced the lowest AIC and the highest adjusted R^2 value (Climate Model 2, AIC = -144.64 , adjusted $R^2 = 0.62$; Climate Model 1, AIC = -141.38 , adjusted $R^2 = 0.59$) (Table 2, Appendix S2: Table S1) and is presented here. Population MISM was strongly associated with species identity ($F_{5,76} = 17.86$, $p < 0.001$); however, no single species produced seeds that differed significantly in mean individual mass from all other species (Appendix S1: Figure S2, Appendix S2: Tables S2 and S3). For example, *S. tortuosus* produced seeds larger than *S. breweri*, *S. hesperidis*, and *S. polygaloides* but not significantly different from *S. barbiger* or *S. glandulosus* (Appendix S1: Figure S2).

Responses of seed mass to climate

Independent of species identity, population MISM was associated with local long-term mean WSS GDD and WSS PPT and with the WSS precipitation anomaly in the year of seed development (Tables 1 and 2). The directions of these effects are described in what follows. Given that WSS GDD and WSS PPT significantly interact to predict seed mass, we chose to focus on describing the interactive effect of these two variables rather than their independent effects because these main effects are not constant across the entire range of the interacting covariate (Engqvist, 2005).

Effect of precipitation anomalies on seed mass

Populations collected during wetter-than-average years (relative to the long-term mean at a given site) produced smaller seeds than those collected during drier-than-average years (Figure 2, Table 1); Climate Model 2 detected a significant negative effect of cumulative WSS precipitation anomalies during the year of seed development on MISM. Estimates from Climate Model 2 indicate that, among populations, seed mass declined by 0.0106 ± 0.0037 mg for every 100-mm increase in precipitation during the year of seed development relative to the long-term mean precipitation at a given site ($F_{1,76} = 8.33$, $p = 0.0051$) (Figure 3, Tables 1 and 2).

Interactive effect of long-term mean growing season length (GDD) and precipitation on seed mass

Climate Model 2 detected a significant interaction between long-term mean WSS GDD and PPT (GDD \times PPT interaction effect: $F_{1,76} = 4.37$, $p = 0.0399$) (Table 2, Appendix S2). While both parameters generally had positive effects on MISM, the strength of this effect for each predictor depended strongly on the values of the other predictor (Figures 3 and 4). For example, the positive effect of WSS GDD on population MISM was stronger among dry sites than among relatively mesic sites (Figure 4a). Similarly, the positive effect of PPT was stronger among sites characterized by short growing seasons (those with low GDD) than among sites with relatively long growing seasons (Figures 3 and 4b).

The Johnson–Neyman interval analysis indicated that growing season length (estimated as WSS GDD) had a significant and positive effect on MISM among relatively dry sites where long-term mean WSS PPT < 803 mm (Figure 4a). Among sites that receive more than 803 mm of average precipitation annually (i.e., relatively wet sites); however, WSS GDD had no effect on MISM. Forty of the 88 sampled populations received an average of < 803 mm of WSS PPT from 1961 to 1990 ($\bar{x} = 786 \pm 247$ mm) (Figure 3) (Love & Mazer, 2021).

The effect of long-term precipitation on MISM depended on the long-term growing season length at a given population's site. Long-term mean WSS PPT had a significant and positive effect on MISM at sites with relatively short growing seasons (those for which WSS GDD < 2221) but had no significant effect among sites characterized by longer growing seasons (Figures 3 and 4b). Thirty-eight of the 88 sampled populations occurred at sites with growing seasons that were longer than 2221

TABLE 1 Parameter estimates for multiple linear regression (Climate Model 2) designed to detect the effect of species identity, long-term mean climatic conditions for winter, spring, and summer (WSS) growing degree-days (GDD) >5°C and cumulative precipitation (PPT, measured in millimeters), and climate anomalies on population mean individual seed mass (mg)

Independent variable	Estimate	SE	t ratio	p > t
Intercept	0.355	0.01954	18.166	<0.001
species [<i>barbiger</i>]	-0.0312	0.06001	-0.52	0.60468
species [<i>breweri</i>]	-0.011	0.03115	-0.677	0.50023
species [<i>glandulosus</i>]	0.14	0.03367	4.157	<0.001
species [<i>hesperidis</i>]	-0.122	0.04425	-2.738	0.00796
species [<i>polygaloides</i>]	-0.14	0.02498	-5.612	<0.001
Long-term mean WSS GDD	4.73×10^{-5}	2.32×10^{-5}	2.041	0.0447
Long-term mean WSS PPT	1.29×10^{-4}	5.79×10^{-5}	2.233	0.0285
WSS GDD anomaly	1.78×10^{-4}	1.51×10^{-4}	1.176	0.2434
WSS PPT anomaly	-1.06×10^{-4}	3.66×10^{-5}	-2.886	0.0051
Long-term mean WSS GDD × Long-term mean WSS PPT	-1.67×10^{-7}	7.96×10^{-8}	-2.09	0.0399
WSS GDD anomaly × Long-term mean WSS PPT	5.67×10^{-7}	4.89×10^{-7}	1.151	0.5035

Note: p-values significant at $\alpha = 0.95$ are bolded. The reference for the main effect of species is *Streptanthus tortuosus*.

TABLE 2 Summary statistics for multiple linear regression (Climate Model 2) designed to detect effects of species identity, long-term mean climatic conditions for winter, spring, and summer (WSS) growing degree-days (GDD) >5°C and cumulative precipitation (PPT, measured in millimeters), and climate anomalies on population mean individual seed mass (mg)

Source of variance	df	SS	F ratio	p-value
Intercept	1	3.22	330.00	<0.001
Species	5	0.87	17.86	<0.001
Long-term mean WSS GDD	1	0.041	4.17	0.0447
Long-term mean WSS PPT	1	0.049	4.99	0.0285
WSS GDD anomaly	1	0.013	1.38	0.2434
WSS PPT anomaly	1	0.081	8.33	0.0051
Long-term mean WSS GDD × long-term mean WSS PPT	1	0.043	4.37	0.0399
WSS GDD × WSS PPT anomaly	1	0.013	1.32	0.5035
Residuals	76	0.74		

Note: p-values significant at $\alpha = 0.95$ are bolded. Akaike information criterion (AIC) = -144.64 and adjusted $R^2 = 0.62$.

cumulative GDD from 1961 to 1990 ($\bar{x} = 2101 \pm 754$) (Love & Mazer, 2021).

DISCUSSION

Geographic variation in seed mass is explained by both long-term climate conditions and precipitation anomalies

Independent of species identity, long-term mean growing season length and cumulative PPT contributed to variation

in MISM among *Streptanthus* populations, corroborating previous work demonstrating that chronic climatic conditions influence the evolution of MISM (Konarzewski et al., 2012; Mazer et al., 2020; Murray et al., 2004). However, among the *Streptanthus* populations examined here, the effect of one variable on MISM depends on the magnitude of the other. The positive effect of growing season length on population MISM was strongest among chronically dry sites (Figure 4a), and the positive effect of increased precipitation was strongest at sites characterized by chronically short growing seasons (Figures 3 and 4b). Given that adaptation represents a long-term evolutionary

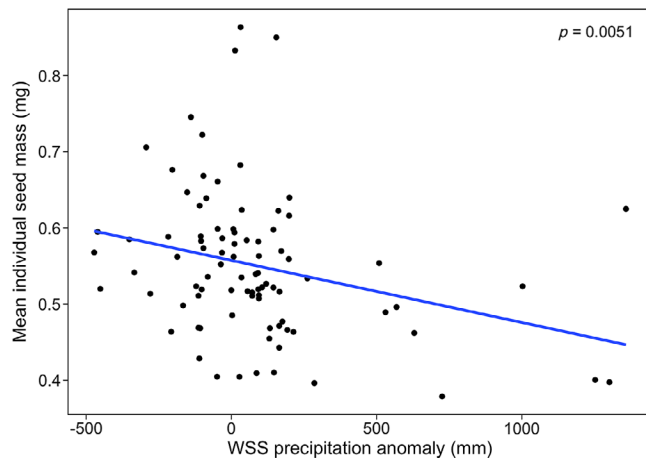


FIGURE 2 Bivariate plot derived from Climate Model 2 showing effect of winter, spring, and summer (WSS) precipitation (PPT) anomalies on population mean individual seed mass independent of other main effects (species identity, long-term mean cumulative WSS PPT, long-term mean cumulative WSS growing degree-days (GDD) $>5^{\circ}\text{C}$, and WSS GDD anomalies)

process that relies on stable environmental conditions, the relationship between seed mass and long-term mean climate detected here likely reflects adaptive responses to chronic climatic conditions during the growing season (Bontrager & Angert, 2016; Mazer et al., 2020; Ramírez-Valiente et al., 2009).

Independent of long-term mean climate, seed mass variation among populations of *Streptanthus* was also explained by WSS PPT anomalies; however, the direction of this effect on seed mass differed from the effect of long-term mean precipitation. Positive values for precipitation anomalies during the year of seed development (i.e., wetter-than-average years) were associated with relatively low population MISM, whereas relatively high values for long-term mean precipitation (i.e., chronically mesic sites) were associated with relatively high population MISM. In other words, populations produced relatively small seeds during wetter-than-average years (Figure 2) but produced relatively large seeds at chronically mesic sites, particularly those with short growing seasons (Figure 3).

Qualitative differences between the direction of the response of mean seed mass to long-term climatic conditions versus climate anomalies suggest that the underlying biological processes driving these patterns are distinct and are operating at different time scales. Responses to short-term climate anomalies likely reflect short-term plastic responses to interannual differences in climate, while responses to long-term mean climate could primarily reflect evolutionary adaptation to long-term mean climatic conditions (Bontrager & Angert, 2016; Mazer et al., 2020; Ramírez-Valiente et al., 2009; Soper Gorden

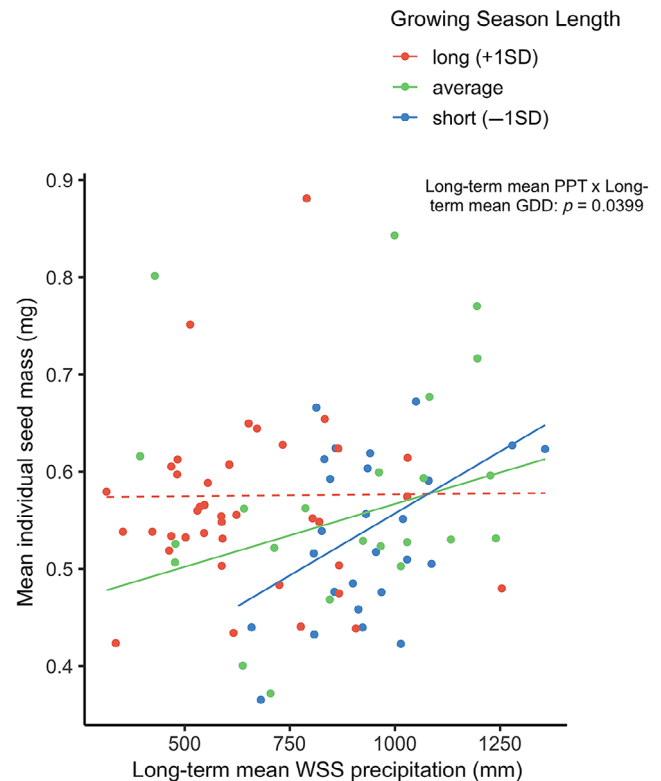


FIGURE 3 Partial effect plot derived from Climate Model 2 demonstrating interaction between long-term mean winter, spring, summer (WSS) growing degree-days (GDD) $>5^{\circ}\text{C}$ and long-term mean WSS precipitation (PPT). The relationship between population mean individual seed mass (MISM) and cumulative WSS PPT is displayed for each of three growing season lengths (mean GDD and GDD ± 1 SD). Each line shows the expected value of population MISM as a function of long-term mean cumulative WSS PPT for a given growing season length. The red dashed line indicates a nonsignificant relationship between the two variables among sites with relatively long growing seasons

et al., 2016). Mazer et al. (2020) similarly detected contrasting effects of long-term mean precipitation and short-term precipitation anomalies on seed mass among 58 wild populations of 6 *Clarkia* (Onagraceae) taxa in California, and although the pattern detected in their study differs qualitatively from that reported here (populations of *Clarkia* produced relatively large seeds in chronically dry environments but relatively small seeds during drier-than-average years), both studies demonstrate that responses to long-term climate may differ from responses to anomalies experienced by populations in the year of seed collection.

The number of populations sampled per species in the current study limited our ability to test for interspecific variation in the response to precipitation anomalies; future studies investigating seed mass or other functional traits should consider assessing such differences as well as their drivers. For example, annuals or short-lived

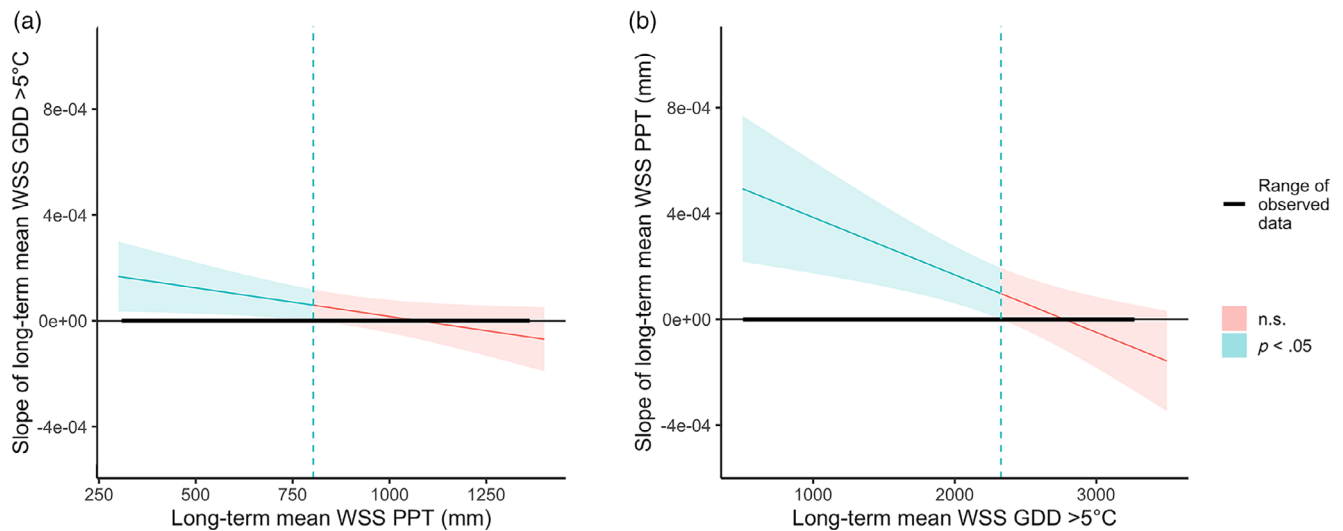


FIGURE 4 Results of Johnson–Neyman interval analysis derived from Climate Model 2, illustrating (a) effects of WSS PPT (moderator) on estimated slope of relationship between long-term mean winter, spring, summer (WSS) growing degree-days (GDD) and population mean seed mass and (b) effects of WSS GDD on estimated slope of relationship between WSS PPT and population mean seed mass. The Johnson–Neyman intervals display how the estimated slope for a given predictor variable (y -axis) depends on the values of the moderator (x -axis). The intervals of the x -variable within which the slope estimates differ significantly from zero ($p < 0.05$) are shown in blue; the intervals within which the slope estimates do not differ significantly from zero are shown in red. The thick portion of the horizontal black line at $x = 0$ indicates the range of observed x -values

perennial species may differ in their phenotypic responses to short-term climate anomalies from longer-lived species, which could ultimately influence community-level attributes and dynamics (Butterfield et al., 2019; Compagnoni et al., 2021). Such studies could shed light on how species' life histories might mediate their responses to climate change and their interactions with sympatric species. Moreover, responses of functional traits to climate anomalies may differ among populations or regions of broadly distributed species, which could generate divergent responses to climate change within species (Pearson et al., 2021). These topics remain relatively unexplored but represent promising avenues of research by which to identify the circumstances under which population mean phenotype is likely to change in response to local climate anomalies.

We also recognize that the uneven sampling of populations across species may have influenced the patterns detected here. For example, *Streptanthus tortuosus*—the species for which we sampled the most populations—will likely have the strongest influence on the outcome of the models presented here. This kind of sampling imbalance means that, if there is a difference among *Streptanthus* species in the direction or magnitude of their responses to local climatic conditions, the best-sampled species will have a disproportionate effect on a linear model's parameter estimates and, consequently, have the strongest influence on any inferences derived from these models.

Selection on seed mass during winter, spring, summer growing season

Natural selection on seed mass may operate during multiple life stages, contributing to intraspecific or intrageneric variation in seed mass. In this study, long-term mean climatic conditions during the growing season (GDD and PPT), when seeds were developing and maturing, interacted to predict population mean seed mass. The fact that this interaction was detected between long-term mean cumulative GDD and PPT but not between the anomalies for these variables supports the hypothesis that the response to long-term mean climate likely reflects adaptive responses of mean seed mass to chronic conditions during the growing season. Examining this interaction can help us to understand the selective forces that may act to generate seed mass variation among populations of *Streptanthus*.

In this study, the positive effect of long-term mean precipitation on population MISM depended on the long-term mean length of the growing season at a given population's location, revealing two patterns of potential adaptive significance (Figure 3). Among populations receiving a mean long-term WSS PPT < 1050 mm, sites characterized by long growing seasons produced relatively large seeds compared to those with short growing seasons. This result is consistent with other studies that detected a positive relationship between seed size and growing season length among populations within species

(Crouch & Vander Kloet, 1980; Daws et al., 2004; de Frenne et al., 2010; Galen & Stanton, 1993; Li et al., 1998). Positive covariation between seed mass and latitude (which is positively correlated with temperature and growing season length) has also been detected among plant species globally (Marshall et al., 2018; Moles et al., 2007). These patterns are consistent with the so-called developmental window hypothesis, which proposes that the observed negative association between seed size and latitude among plant species globally is generated by selection favoring large seeds at sites with long growing seasons (Marshall et al., 2018; Moles et al., 2007). A longer growing season may facilitate the evolution of larger seeds because maternal plants experience a longer period of conditions amenable to growth during which to provision seeds, and these larger seeds may provide a benefit to seedlings by allowing seedlings to germinate and to establish roots relatively rapidly (Benard & Toft, 2007; Lloret et al., 1999; Marshall et al., 2018; Seiwa et al., 2002). In contrast to plants, among many animal taxa, offspring tend to be larger at higher latitudes where temperatures are colder and growing seasons shorter (Marshall et al., 2018). This pattern is likely generated by selection favoring larger offspring in environments in which a large size mitigates the high cost of development at colder temperatures (Pettersen et al., 2019). These contrasting patterns suggest that selection generates opposing clines in offspring size along temperature and growing season length gradients among plants and many groups of animals.

In this study, we also found that the positive effect of long-term mean precipitation on seed mass was strongest at sites with relatively short growing seasons (Figures 3 and 4). Among these sites, populations produced relatively large seeds at sites receiving relatively high precipitation. This suggests that precipitation may facilitate the production of large seeds, but only at sites with short growing seasons. Where ample precipitation is available for maternal investment in seeds, selection may favor the production of large seeds because large seeds produce robust seedlings with well-developed root systems that can boost seedling survival and individual fitness (Benard & Toft, 2007; Lloret et al., 1999; Volis & Bohrer, 2013). Why this pattern was observed here only at sites with low GDD values remains unclear and merits further study. However, these results highlight the need to consider how interactions between climatic variables influence functional traits when modeling the consequences of climate change on demographic processes.

Potential consequences of climate change on seed mass

This is one of the first studies to demonstrate that long-versus short-term climatic conditions can have contrasting

effects on population mean seed mass (cf. Mazer et al., 2020). The study contributes to our broader understanding of how climate drives trait variation across landscapes due to long-term (e.g., local adaptation) and short-term (e.g., phenotypic plasticity) processes. In addition, the results presented here have important implications for predicting responses of seed mass to climate change. The opposing response of seed mass to long- versus short-term variation in climate detected in the current study may represent evidence of countergradient or nonadaptive plasticity, whereby the plastic responses of seed mass to interannual variation in precipitation differ from adaptive responses to chronic precipitation regimes (Ensing & Eckert, 2019). If this is the case, then the plastic responses of seed mass to interannual variation in precipitation generated by future climate change may constrain adaptation to long-term changes in precipitation regimes, which could hinder population persistence (Eckhart et al., 2004). In contrast, cogradient plasticity, whereby plastic and adaptive responses to environmental variation occur in the same direction, may facilitate adaptive responses to climate change.

Studies like this one of geographic variation that explicitly test for the independent effects of long-term climate conditions versus climate anomalies on life history traits can be used to seek evidence for co- or countergradient plasticity using field-collected trait data. These studies also contribute to our limited understanding of both the short- and long-term effects of climate change on life history traits and, in turn, on their cascading influence on subsequent life history stages (de Frenne et al., 2010; Etterson, Franks, et al., 2016; Gremer, Wilcox, et al., 2020). The analytical framework presented in this study can be applied to many different traits and taxa across a variety of ecosystems. These types of studies are a critical first step toward detecting potential cases of co- or countergradient plasticity, which can then be more rigorously tested with reciprocal transplants along environmental gradients (Ensing & Eckert, 2019).

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data and code (Love & Mazer, 2021) are available in Zenodo at <https://doi.org/10.5281/zenodo.5102713>. This is not novel code, and the packages used to conduct all analyses are cited in the manuscript.

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