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Clinal adaptation and adaptive plasticity in *Artemisia californica*: implications for the response of a foundation species to predicted climate change

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Abstract

Local adaptation and plasticity pose significant obstacles to predicting plant responses to future climates. Although local adaptation and plasticity in plant functional traits have been documented for many species, less is known about population-level variation in plasticity and whether such variation is driven by adaptation to environmental variation. We examined clinal variation in traits and performance – and plastic responses to environmental change – for the shrub *Artemisia californica* along a 700 km gradient characterized (from south to north) by a fourfold increase in precipitation and a 61% decrease in interannual precipitation variation. Plants cloned from five populations along this gradient were grown for 3 years in treatments approximating the precipitation regimes of the north and south range margins. Most traits varying among populations did so clinally; northern populations (vs. southern) had higher water-use efficiencies and lower growth rates, C : N ratios and terpene concentrations. Notably, there was variation in plasticity for plant performance that was strongly correlated with source site interannual precipitation variability. The high-precipitation treatment (vs. low) increased growth and flower production more for plants from southern populations (181% and 279%, respectively) than northern populations (47% and 20%, respectively). Overall, precipitation variability at population source sites predicted 86% and 99% of variation in plasticity in growth and flowering, respectively. These striking, clinal patterns in plant traits and plasticity are indicative of adaptation to both the mean and variability of environmental conditions. Furthermore, our analysis of long-term coastal climate data in turn indicates an increase in interannual precipitation variation consistent with most global change models and, unexpectedly, this increased variation is especially pronounced at historically stable, northern sites. Our findings demonstrate the critical need to integrate fundamental evolutionary processes into global change models, as contemporary patterns of adaptation to environmental clines will mediate future plant responses to projected climate change.

Keywords: artemisia, clinal adaptation, common garden, environmental variability, latitudinal gradients, phenotypic plasticity, precipitation, resource gradients

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Introduction

The study of species adaptation to the biotic and abiotic environment has taken on a new urgency because of anticipated global climate change; evidence of local adaptation demonstrates the importance of past evolutionary processes for contemporary ecological dynamics, and suggests a key role for adaptation in plant responses to a changing environment (Davis *et al.*, 2005; Woods *et al.*, 2012). Latitudinal gradients in environmental conditions often result in intraspecific clinal variation or ecotypic differentiation in plant traits (Clausen *et al.*, 1940; Linhart & Grant, 1996; Thompson *et al.*, 2007). In particular, abiotic gradients can drive genetically based clinal variation in growth (Lieth,

1973; Hsu *et al.*, 2012), phenology (Jonas & Geber, 1999) and herbivore defense traits (Cunningham *et al.*, 1999; Woods *et al.*, 2012) among populations of the same species. Such genetically based clines in species functional traits provide unique opportunities for documenting co-variance among functional traits and the environment, and can decipher the processes underlying adaptation and responses to environmental change.

In contrast to the convincing evidence that local adaptation of plant populations is a widespread phenomenon (Dudley, 1996; Linhart & Grant, 1996; Kawecki & Ebert, 2004; but see Leimu & Fischer, 2008), less is known about how plasticity in plant traits and performance might vary across a species' range and whether such variation in plasticity correlates to geographic variation in environmental variability (Gianoli, 2004). More variable environments should select for higher levels of trait plasticity (Via & Lande, 1985;

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Sultan, 1987; Gabriel & Lynch, 1992), allowing a species to maximize fitness under optimal environmental conditions and better tolerate abiotic stress (Sultan, 2001; Sultan & Spencer, 2002). Plasticity is likely to be important for short-term responses to future climate change to the extent that it allows species persistence (vs. potentially rapid local extinctions) for a longer period during which evolutionary adaptation may occur (Draghi & Whitlock, 2012). Intraspecific variation in plasticity in performance (e.g., growth and reproduction) is of particular interest for determining species-level responses to future environmental change and whether the ability to respond to such change is variable among populations, yet there are few data on the relationship between past environmental variability and current levels of plasticity (Gianoli, 2004; Valladares *et al.*, 2007).

Water availability is a central feature of any environment and is perhaps the key selective force shaping the evolution of plants in arid environments (Niklas, 1997) and influencing traits related to primary production (Larcher, 2003; Grant *et al.*, 2005; Nicotra *et al.*, 2007), reproductive output (Sultan & Bazzaz, 1993; Thompson, 2005), phenology (Woods *et al.*, 2012), and trophic interactions (e.g., plant defenses; Cunningham *et al.*, 1999; Stamp, 2003). Although a few studies have documented population variation in trait plasticity in response to manipulated water availability (Volis *et al.*, 2002; Heschel *et al.*, 2004; Grant *et al.*, 2005), quantitative measures of environmental variability and associations between such variability and levels of plasticity have rarely been analyzed (Gianoli, 2004). Altered precipitation patterns, including changes in annual precipitation and interannual precipitation variability, are one of the principal aspects of global environmental change impacting biological communities (Easterling, 2000; Weltzin *et al.*, 2003; Tylianakis *et al.*, 2008).

Mediterranean plant communities may be particularly sensitive to altered precipitation as they routinely experience water stress during seasonal (summertime) droughts that characterize this climate type and impose major constraints on plant growth, reproduction, and survival (Thompson, 2005; Thompson *et al.*, 2007). California's Mediterranean climate is predicted to become substantially warmer, with increased interannual precipitation variability and extended droughts of particular concern (Hayhoe *et al.*, 2004; Luers *et al.*, 2006; Cayan *et al.*, 2008). California's coastal environment is characterized by steep gradients in temperature and precipitation as well as precipitation variability thus making it an ideal location to study the impacts of such gradients on existing patterns of clinal adaptation and plasticity across the full range of projected future climatic conditions.

In this study, we examine clinal variation and phenotypic plasticity in plant traits and whole-plant performance of the long-lived woody shrub *Artemisia californica* Less. in coastal California. This species' range spans a 700 km (6° latitudinal) gradient characterized (from south to north) by a fourfold increase in mean annual precipitation and a 61% decrease in interannual precipitation variability. To isolate the effects of precipitation from other clinally varying parameters, we grew plants from across this range in a single common garden where we manipulated water to mimic the precipitation regimes of the northern and southern ends of the species' range. Measuring plant performance and functional traits relevant to interactions with both the abiotic (water stress, nutrient acquisition) and biotic (herbivory) environment, we addressed the following questions:

1. Do populations spanning the range of *A. californica* differ in physiological, chemical, and phenological traits and plant performance and is such variation clinal?
2. Do plant traits and performance respond plastically to the experimental manipulation of precipitation that mimics environmental conditions experienced at the two margins of the species' range?
3. Does the degree of plasticity in traits and plant performance vary among populations and, if so, does this variation correspond to the pattern of environmental variation of the source population sites?

By testing for clinal variation in both functional traits and plastic responses to an altered precipitation regime, this study addresses how contemporary patterns of adaptation to this steep environmental cline are likely to mediate future plant responses to projected climate change.

Materials and methods

Study system

California Sagebrush (*Artemisia californica* Less., Asteraceae) is a foundation species (*sensu* Dayton, 1972) in coastal sage scrub (CSS) habitats. *Artemisia californica* ranges approximately 1000 km along a fivefold precipitation gradient from Northern Baja, Mexico (average annual precipitation: 20 cm) to Mendocino County, California (average annual precipitation: 103 cm) at low elevations (<800 m) along the coast. Coastal sage scrub vegetation is highly fragmented throughout this range and has been reduced to 10–15% of its historical distribution in the past several decades as a result of land-use change, and is thus considered a critically threatened ecosystem (Davis *et al.*, 1994; Talluto & Suding, 2008). This study, based upon five populations of *A. californica* distributed over 700 km in southern and central California (32.5–37.5° latitude), represents 70%

of its range and includes 85% of the precipitation gradient across which it occurs (Table 1).

To examine latitudinal patterns in mean annual precipitation (MAP) and temperature (MAT) and interannual variation in precipitation (precipitation CV) and temperature (temperature CV), we analyzed climate data from 24 weather stations distributed across the gradient (Table S1). This analysis showed that progressing from south to north, the environment becomes colder and wetter with decreases in precipitation variability, but no detectable pattern for temperature variability (Table 1a). The climatic data from our five source populations were representative of this overall gradient (Table 1b), although MAT and precipitation CV for these particular sites did not exhibit a monotonic pattern across the gradient. Our analyses also suggest that the increase in interannual precipitation variability predicted by most global change models (Easterling, 2000; Weltzin *et al.*, 2003; Meehl *et al.*, 2007) is already underway. We compared interannual precipitation CV from the 20 stations for which we had long-term data both pre- and post-1980 and found that post-1980 values were higher than pre-1980 values at 19 of 20 coastal climate stations (Table S1–II), with an overall increase in CV of $16 \pm 3\%$ (from 0.349 to 0.411; $F_{1,19} = 19.81$, $P < 0.0003$). Moreover, the magnitude of this increase in CV shows a trend with latitude ($F_{1,19} = 2.72$, $P = 0.1163$; $R^2 = 0.1314$), with variability increasing more in the north than the south, such that the southernmost three stations increased 4% in CV (range 0.8% to 8.9%) whereas the northernmost three stations increased 29% in CV (range 18% to 47%). When two additional climate stations further north of the *A. californica* distribution are included in the analysis (to Fort Bragg, 39.3° latitude), the pattern is significant ($F_{1,21} = 6.65$, $P = 0.0179$; $R^2 = 0.2496$). Thus, it is the historically most stable sites that may be experiencing the greatest increases in variability.

Experimental protocols

Common garden design. In spring 2008, we collected 20 cuttings from 20 *A. californica* plants in each of five source populations distributed along the gradient described above. To minimize nongenetic (maternal-like) effects associated with plants cloned from cuttings (Roach & Wulff, 1987), plants were grown in the greenhouse and field for a total of 24 months before traits were measured (see below). In addition, an on-going experiment with seed-grown plants (J.D. Pratt, unpublished results) confirms the results presented here for plant growth rate (the only trait as yet measured).

Plant cuttings were dipped in a 20% solution of Dip 'N Grow Root Inducing Concentrate (Dip 'N Grow Inc., Clackamas, OR) and planted in horticultural perlite for 6 weeks. Rooted cuttings were then transplanted to individual pots containing a soil mixture of equal parts silica sand, redwood compost, peat moss, and pumice and grown in a greenhouse for 9 months. In December 2008, these cuttings (surviving plants $N = 152$; SD33 = 17, SM34 = 43, CAM36 = 33, SC37 = 31, GG38 = 28) were planted into common garden plots at a site in Newport Beach, CA (Table 1b). This site, part of the Upper Newport Bay Ecological Preserve, is a degraded

patch of upland habitat approximately 100 m from Newport Bay and 6 km inland from the ocean coastline. The site was historically composed of CSS and grassland matrix, including *A. californica*, but currently is covered by a mix of non-native grasses and forbs with a few native shrubs interspersed. Intact CSS habitat is found in patches throughout the areas adjacent to the common garden.

The common garden consisted of three blocks, each containing a pair of 5×6 m plots, with 2 m between plots and 4 m between blocks. The total sample size for each source population (see above) was evenly distributed among and randomized within these six plots. Plants were watered minimally through September 2009 to ensure establishment and survival. In December 2009, we implemented a precipitation manipulation at the plot level using overhead sprinklers to supply supplemental water to one plot within a block (hereafter *High* precipitation plots), as compared with the remaining plot which received ambient precipitation (*Low* precipitation plots). We applied water equivalent to the precipitation difference between the southern and northern extremes of the species range (70 cm annually; WRCC, 2012). We measured water addition by placing six 1 l open containers in a grid within each plot and calculating the average depth of water (cm) each time the treatment was applied. We mimicked the seasonal cycles of precipitation in our Mediterranean climate to apply supplemental water, with 56% applied in winter (December–February, 13 cm month⁻¹), 22% applied in spring (March–May, 5 cm month⁻¹), 1.5% applied in summer (June–August, 0.75 cm month⁻¹), and 20.5% applied in fall (September–November, 4.5 cm month⁻¹).

Plant measurements. We measured a suite of functional traits (hereafter, 'leaf-level traits') of recognized importance for interactions with the abiotic and biotic environment (Cornelissen *et al.*, 2003), flowering phenology, and plant performance (e.g., plant size, flower production) for common garden plants.

Leaf-level traits. In April 2010, during peak growing season, we collected 30 fully expanded leaves from each of a subset of plants; ten leaves were used to assess specific leaf area (SLA) and percent water content (PWC; $N = 111$ plants; SD33 = 17, SM34 = 27, CAM36 = 24, SC37 = 21, GG38 = 22), 10 leaves were used to assess plant defensive chemistry (i.e., terpenes; $N = 123$ plants; SD33 = 17, SM34 = 43, CAM36 = 33, SC37 = 31, GG38 = 28), and the remaining 10 leaves for carbon and nitrogen isotopic analysis ($N = 109$ plants; SD33 = 16, SM34 = 25, CAM36 = 25, SC37 = 21, GG38 = 22).

For SLA and PWC, freshly picked leaves were immediately placed on ice and kept cool until they were scanned and weighed (wet weight) later that same day. Leaves were then dried at 60 °C for 72 h and weighed again (dry weight). Leaf area (cm²) was determined from scanned images using ImageJ software (Rasband, 2008). SLA was calculated as cm² g⁻¹ dry weight and PWC as (wet weight–dry weight)/wet weight.

To assess leaf carbon (C) and nitrogen (N) content, C and N isotopic ratios, and integrated water-use efficiency (hereafter WUE), leaves were dried at 60 °C for 72 h and then ground to

Table 1 a) Relationships among the 24 climate stations and latitude for average annual precipitation and temperature and interannual variation in precipitation and temperature, b) Location and climate data for five *A. californica* source populations and the common garden site

Location information		Mean annual precipitation data				Mean annual temperature data							
(a) Description of gradient		MAP vs. latitude		CV vs. latitude		MAT vs. latitude		CV vs. latitude					
Climate stations ($N = 24$) across latitude in California		Latitude range	Elevation	Annual avg	Years of record**	CV	Driest year	Wettest year	Annual avg	Years of record**	CV	Coldest year	Warmest year
See Table S1 for station list	32°36'N–38°31'N	$P < 0.0001$ $R^2 = 0.6072$	95 m	25 cm	98 (1914–2011)	0.410	9 cm (1953)	63 cm (1941)	17.3 °C	98 (1914–2011)	0.024	15.3 °C (1933)	19.6 °C (1984)
	117°14'W		80 m	32 cm	47 (1937–2011)	0.476	10 cm (1989)	65 cm (1998)	16.2 °C	39 (1937–2010)	0.019	14.9 °C (1962)	17.8 °C (1984)
(b) Description of population source environments and common garden site													
Site name	Lat/Long	Elevation	Annual avg	Years of record**	CV	Driest year	Wettest year	Annual avg	Years of record**	CV	Coldest year	Warmest year	
**Scripps Coastal Reserve, La Jolla (SD33)	32°52'N; 117°14'W	95 m	25 cm	98 (1914–2011)	0.410	9 cm (1953)	63 cm (1941)	17.3 °C	98 (1914–2011)	0.024	15.3 °C (1933)	19.6 °C (1984)	
Santa Monica Mountains National Recreation Area, Santa Monica (SM34)	34°03'N; 118°59'W	80 m	32 cm	47 (1937–2011)	0.476	10 cm (1989)	65 cm (1998)	16.2 °C	39 (1937–2010)	0.019	14.9 °C (1962)	17.8 °C (1984)	
**Rancho Marino Reserve, Cambria (CAM36)	35°31'N; 121°04'W	60 m	50 cm	49 (1938–1997)	0.392	20 cm (1990)	106 cm (1969)	12.6 °C	27 (1938–1975)	0.022	11.5 °C (1946)	13.6 °C (1963)	
Wilder Ranch State Park, Santa Cruz (SC37)	36°58'N; 122°07'W	20 m	74 cm	76 (1893–2011)	0.318	31 cm (1929)	152 cm (1983)	13.8 °C	106 (1893–2011)	0.018	12.6 °C (1955)	15.4 °C (1926)	
Rodeo Beach, Golden Gate National Recreation Area, San Francisco (GG38)	37°50'N; 122°32'W	57 m	95 cm	57 (1940–2011)	0.297	43 cm (1976)	176 cm (1983)	14.5 °C	78 (1902–2011)	0.025	12.4 °C (1922)	16.4 °C (1997)	
Common garden: Newport Beach, CA	33°39'N; 117°53'W	16 m	28 cm	65 (1921–2011)	0.465	13 cm (1953)	71 cm (1978)	16.1 °C	64 (1921–2011)	0.021	14.6 °C (1933)	18.0 °C (1984)	

*Units for slope for precipitation = cm/° latitude; for temperature = °C/° latitude; for CV = CV/° latitude.

**Number indicates total number of years used in analysis out of the range of years on record (in parenthesis). Any year with a month that had more than 5 days of data missing was excluded from the calculations of annual averages.

a fine powder using a Wig-L-bug grinding mill (International Crystal Laboratories, Garfield, NJ). Approximately 1 mg of this homogenized powder was then packed into 5 × 9 mm tins. Elemental analysis (Fisons Instruments 1500) and mass spectrometry (Delta plus XL, Thermo Finnigan, Asheville, NC) was then performed at the UC-Irvine Stable Isotope Ratio and Mass Spectrometry Facility.

In April 2011, predawn (0400–0600 h) and mid-day (1130–1330 h) water potentials (ψ_{Pd} and ψ_{Md} , respectively) were assessed for a subset of plants ($N = 40$, 4 per source population/treatment) using a 10 cm sun-exposed stem cutting collected from the top of the shrub; measurements were performed with a Scholander-type pressure chamber (PMS Instrument Company, Albany, OR) immediately after cutting. Water potential measurements, while taken on stem cuttings, are grouped as leaf-level traits for simplicity in presentation and discussion as all other measured traits are either on leaves or whole plant canopies.

To assess terpene concentrations, which serve as important defenses against herbivores (Eisner, 1964; Whittaker & Feeny, 1971; Mabry & Gill, 1979), haphazardly collected leaves were immediately placed in 2 ml *n*-hexane, sonicated for 10 min and soaked at room temperature. After seven days, extracts were poured off and stored at -80°C until analysis by gas chromatography and mass spectrometry (GC-MS) and leaf material was dried at 60°C for 72 h and weighed. For terpene analysis, 10 μl of an internal standard solution (0.13 $\mu\text{l ml}^{-1}$ *m*-xylene in *n*-hexane) was added to 90 μl of each sample extract. Samples were injected (4 μl) onto a GC-MS (Trace MS+, ThermoFisher Scientific, Asheville, NC) fitted with a 30 m × 0.25 mm × 0.25 μm film thickness DB-5 fused silica column (J&W Scientific, Folsom, CA). The GC was operated in splitless mode with helium as the carrier gas (flow rate 1 ml min^{-1}). The GC oven temperature program was as follows: 1 min hold at 50°C , $5^{\circ}\text{C min}^{-1}$ ramp to 180°C , $20^{\circ}\text{C min}^{-1}$ ramp to 290°C , and 1 min hold at 290°C . The mass spectrometer was operated in electron ionization mode and data were collected between m/z 50–650. We identified mono- and sesquiterpenes in our samples and examined relative investment in defense by calculating the normalized area per dry weight (peak area/area of internal standard/dry weight of leaf material) for all terpenoid compounds detected.

Phenology. *Artemisia californica* flowers from approximately April–December. We conducted weekly phenology surveys (flowering or not) and monthly inflorescence counts on all plants from April–December 2011. Data from monthly counts were used to assess the average flowering date (AFD) for each plant. The AFD is a weighted average of the dates flowers were produced throughout the season (cf. Nuismer & Cunningham, 2005). To calculate flowering duration and eliminate outliers (i.e., a few plants that produced a few flowers very early or very late in the season), we estimated the dates between which 10% and 90% of total flowers had been produced and subtracted these values (other percent ranges, e.g., 15–85%, produced qualitatively identical results). We considered the date at which 10% of flowers had been produced as the onset of flower production.

Plant performance. We measured plant size eight times between March 2009–November 2011 on all experimental plants ($N = 152$ at conclusion of experiment; SD33 = 17, SM34 = 43, CAM36 = 33, SC37 = 31, GG38 = 28) by calculating the volume for the minimally sized cylinder needed to contain the plant (height × radius $1 \times$ radius $2 \times \pi$) multiplied by the proportion of the cylinder volume occupied by the plant (visual estimate to the nearest 10% cover).

We assessed total flower production as a proxy for fitness. In October 2011 we collected ten inflorescences from each of 96 flowering plants equally representing the five source populations in both precipitation treatments and counted the number of flowers per inflorescence under a dissecting scope. Each flower is capable of producing a single seed. Inflorescences varied in flower number (range 20–40) with the number of flowers per inflorescence differing among the five source populations ($F_{4,82} = 7.64$, $P < 0.0001$). Although there was no detectable effect of the precipitation treatment ($F_{1,2} = 2.68$, $P = 0.2431$), all populations tended to have more flowers per inflorescence in the high precipitation treatment. Accordingly, we multiplied inflorescence counts by the source population mean within each precipitation treatment to calculate flower production each month and total overall flower production for 2011.

Statistical analyses

We tested for main effects of source population, precipitation treatment, and their interaction on all measured traits. The number of functional traits ($N = 12$) and performance variables ($N = 2$) was large and showed patterns of co-variance (Table S2), thus raising concern of inflated type I error (Garcia, 2004). A principal component (PC) analysis can reduce the dimensionality of such datasets to analyze effects on a reduced number of PC axes. Yet this approach was problematic here; growth (only) required a repeated measures analysis, and sample sizes varied among dependent variables (e.g., $N = 40$ for water potential vs. $N = 152$ for plant growth and flowering, and $N = 26$ for plants on which all traits were measured), meaning that a PC analysis must exclude either replicates or traits. We used PROC PRINCOMP in SAS (v. 9.2) to conduct a PC analysis that was based on the final growth measurement and excluded the two traits with the lowest sample size (water potential measurements) for a sample size of 101 plants. Because of the limitations to this approach, we also conducted univariate analyses and consider these results with several approaches that account for inflated type I error (Garcia, 2004).

A significant source population effect indicates genetic differences among populations, a significant precipitation effect indicates trait plasticity, and a significant source population-by-precipitation interaction indicates differences among populations in the degree

of plasticity. Our measurements of phenotypic plasticity in response to the precipitation manipulation may result from plastic responses that are a direct response to the biotic or abiotic environment, plastic responses associated with ontogenetic drift (i.e., if mean trait values change over plant ontogeny), or some combination of the two (Evans, 1972; Coleman *et al.*, 1994). We report results that do not account for plant size, thus assessing both forms of plasticity. However, analyses that included plant size as a covariate (not shown) produced qualitatively identical results to those presented here.

All analyses were conducted using the MIXED procedure in SAS Version 9.2 (SAS Institute, 2010) specifying the block and precipitation-by-plot interaction as random effects. To meet ANOVA assumptions of normally distributed residuals and homogeneity of variances, plant volume and total flower production were square-root transformed whereas all other variables were untransformed. As plant volume was measured repeatedly throughout the study, we tested for the main and interactive effects of population and treatment on plant volume over time using repeated measures ANOVA. The model was parallel to that described above, with the addition of time ($N = 8$) and all two-way and three-way interactions between time, population, and treatment. Because we found a significant three way interaction between time, population, and treatment in this analysis ($F_{56,141} = 2.99$, $P < 0.0001$), we performed separate two-way ANOVAs as described above for each time point to determine when the main and interactive effects of population and treatment occurred over the course of the experiment.

We tested for a clinal pattern across the latitudinal gradient for all traits (and PC axis scores) where two-way ANOVAs (see above) showed a significant main effect of population by conducting linear regressions between the population means across treatments for that trait and latitude using PROC REG (SAS Institute, 2010). As it was not possible to conduct multiple regression given our sample size ($N = 5$ populations), we conducted separate univariate regressions between population means and MAP and MAT to explore whether patterns in traits were best explained by latitude or one of these individual environmental factors by qualitatively comparing R^2 values. Although we report unweighted regressions here, weighted least squares regressions (Carroll & Ruppert, 1988) produced qualitatively identical results to those reported.

For two-way ANOVAs with a significant population-by-precipitation interaction, we conducted linear regressions between population means and latitude separately for each treatment. As this interaction indicates variation in plasticity among populations, we also

tested for clinal variation in plasticity, quantifying plasticity as the precipitation effect size using the log response ratio ('LRR' = $\text{Ln}[\text{high}/\text{low}]$; Hedges *et al.*, 1999) and regressing LRR values on latitude. To test the hypothesis that plasticity should be locally adapted to environmental variability we then regressed LRR values on population source site precipitation CV.

Results

The results of the PC analysis (Appendix A) were difficult to interpret in two respects; the first four PC axes explained only 68% of the multivariate variation (and it required eight axes to exceed 90%), many variables loaded onto multiple axes and, as a result, the axes were not clearly defined by distinct sets of variables. Accordingly, we focus here on the results of univariate analyses (see below), although we note these were largely concordant with analyses of the PC axes (Appendix A). We conclude our presentation of results with an evaluation of the likely significance of these univariate analyses with respect to inflated type I error (Garcia, 2004).

Plant traits

Effects on leaf-level traits. We did not find a significant source population-by-precipitation treatment interaction for any measured leaf-level trait (Table 2a) and therefore only report main effects below. In all but one case, when ANOVAs showed significant effects of source population, that variation was clinal according to regressions with the five population means and latitude (Table 2a, S3).

We found significant effects of the precipitation treatment on leaf percent water content (PWC) and specific leaf area (SLA) but no effect of source population (Table 2a). Specifically, leaf PWC increased 8% and SLA increased 18% from the low to high precipitation treatment (Fig. 1a,b). Predawn and mid-day water potentials did not differ between source populations or precipitation treatments (Table 2a; Fig. 1c). Stable isotope analysis of intrinsic water-use efficiency (WUE) showed significant clinal variation with WUE increasing 5% from southernmost to northernmost populations (i.e., a smaller Delta value indicates greater WUE; Fig. 1d). Surprisingly, watering did not have a significant effect on WUE (Table 2a). Leaf $\delta^{15}\text{N}$ did not differ among source populations or precipitation treatments (Table 2a; Fig. 1e). There was significant clinal variation in leaf percent N and C : N ratio (Table 2a, S3); percent N increased 25%, while C : N decreased 21% from southernmost to northernmost populations (Fig. 1f,g). Watering increased percent N by 22% and

Table 2 Statistics for main and interactive effects of source population (Site) and precipitation treatment (Treat) on *A. californica* (a) traits, (b) phenology, and (c) plant performance. Significant *P*-values ($P < 0.05$) are shown in bold. Where ANOVAS indicated significant differences among source populations (but no source population \times precipitation treatment interaction), we tested for clinal patterns by regressing population trait means on source site mean annual precipitation (P), mean annual temperature (T), and latitude (L). Where ANOVAS indicated significant source population-by-precipitation treatment interactions (i.e., variation in plasticity), we tested for clinal patterns by regressing population trait means on latitude separately within the high (LH) and low (LL) precipitation treatments. In addition, we regressed plasticity (the log response ratio, or effect size of precipitation) on both latitude (L) and precipitation coefficient of variation (CV). Significant clinal regressions ($P < 0.05$) are indicated next to the relevant ANOVA results with letters indicating which clinal variables were significant. Detailed regression statistics are presented in Table S3

Variable	Site	Treat	Site*treat
	$F_{DF}(P)$	$F_{DF}(P)$	$F_{DF}(P)$
(a) Leaf-level traits			
Percent water content	2.31 _{4,97} (0.0634)	44.31 _{1,2} (0.0218)	0.77 _{4,97} (0.5456)
Specific leaf area	0.85 _{4,97} (0.4994)	20.26 _{1,2} (0.0460)	0.89 _{4,97} (0.4722)
Water potential, predawn	2.08 _{4,28} (0.1096)	1.52 _{1,1} (0.4338)	2.01 _{4,28} (0.1202)
Water potential, mid-day	1.22 _{4,28} (0.3228)	0.02 _{1,1} (0.9033)	0.71 _{4,28} (0.5909)
d15N	0.52 _{4,95} (0.7241)	11.98 _{1,2} (0.0743)	0.23 _{4,95} (0.9232)
% Nitrogen	6.16 _{4,95} (0.0002), P,L	36.17 _{1,2} (0.0266)	0.96 _{4,95} (0.4312)
C : N	5.78 _{4,95} (0.0003), P,L	41.18 _{1,2} (0.0234)	0.70 _{4,95} (0.5910)
WUE (Delta)	6.97 _{4,95} (<0.0001), P,T,L	8.15 _{1,2} (0.1039)	0.16 _{4,95} (0.9583)
Monoterpene abundance	3.69 _{4,107} (0.0075)	0.05 _{1,2} (0.8434)	0.31 _{4,107} (0.8705)
Sesquiterpene abundance	3.33 _{4,107} (0.0131)	4.82 _{1,2} (0.1592)	0.54 _{4,107} (0.7043)
(b) Phenology			
Flowering duration	6.79 _{4,135} (<0.0001)	7.21 _{1,2} (0.1152)	1.42 _{4,135} (0.2297)
Average flower date	54.75 _{4,135} (<0.0001)	0.84 _{1,2} (0.4561)	7.14 _{4,135} (<0.0001), LH
(c) Performance			
Volume, 44 months	4.20 _{4,137} (0.0031)	34.54 _{1,2} (0.0278)	2.48 _{4,137} (0.0465), LH, CV
Total flower production	0.33 _{4,135} (0.8592)	28.22 _{1,2} (0.0337)	3.38 _{4,135} (0.0113), CV

decreased C : N by 21% (Fig. 1f,g), a change in accordance with the clinal pattern of population trait values across the precipitation gradient.

Source populations varied significantly in their relative investment in both mono- and sesqui-terpenoid defenses (Table 2a; Fig. 1h,i). Investment in monoterpenes increased 156% from southernmost to northernmost populations; however, clinal regressions were not significant (Table S3). Precipitation did not affect mono- or sesqui-terpene production (Table 2a).

Effects on phenology. There was significant, clinal variation among source populations in average flowering date (AFD) with northern populations flowering 30–50 days earlier than southern populations (Fig. 2a), but no main effect of precipitation treatment (Table 2b, S3). A significant source population-by-precipitation treatment interaction indicated population variation in AFD plasticity (LRR effect size) in response to precipitation (Table 2b). Three populations exhibited a high degree of plasticity in AFD; SD33 and SM34 populations shifted their flowering 14 and 10 days earlier, respectively, in response to watering, whereas SC37 shifted flowering almost 20 days later in response to

watering (Fig. 2a). CAM36 and GG38 populations did not exhibit plasticity in flowering time. Plasticity in AFD did not exhibit a clinal pattern with either latitude or precipitation CV (Table S3; Fig. 3a).

There was a significant effect of source population on flowering duration (Table 2b). Variation among source populations was not clinal, rather one population (SC37) began flowering, albeit minimally, an average of 25 days earlier than all other populations (Table S3, Fig. 1j). There was no effect of precipitation treatment or a source population-by-precipitation interaction on flowering duration (Table 2b).

Plant performance

Effects on growth. We found a significant three-way interaction between source population, precipitation treatment and time ($F_{56,141} = 2.99$, $P < 0.0001$; Fig. S1) on plant growth, therefore, we examined the main and interactive effects of source population and precipitation separately for each time point. At all time points there was significant, clinal variation among source populations in plant size (Table S4), with southernmost populations having twice the volume of northernmost

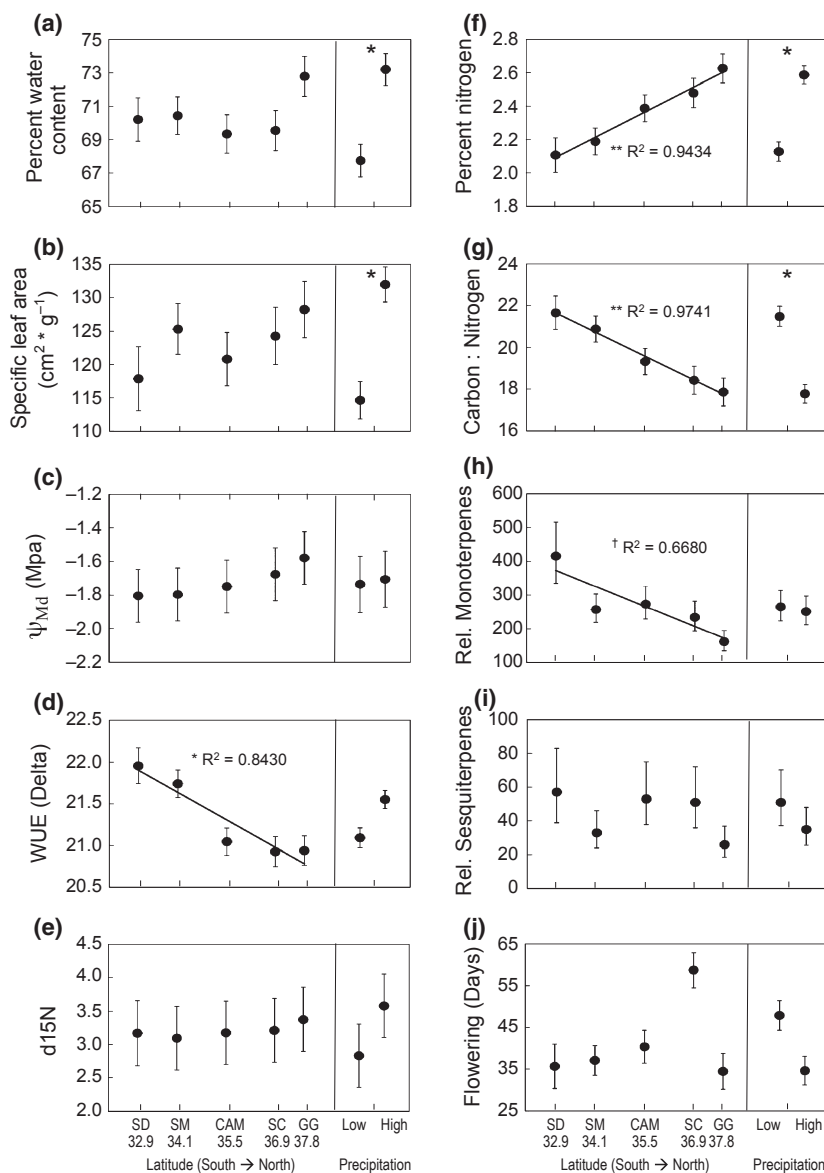


Fig. 1 Source population ($N = 5$) and treatment ($N = 2$) means \pm SE for morphological, physiological and chemical traits measured on common garden plants. For all traits where ANOVA results indicated significant differentiation among source populations and that variation was clinal, it is indicated with regression lines using the five population means and latitude. Symbols next to R^2 values indicate the level of significance of the regression: † = $0.05 < P < 0.10$, * $P < 0.05$, ** $P < 0.01$ and a * indicates a significant difference between the precipitation treatments. We did not find a significant source population-by-precipitation interaction for any traits shown in Fig. 1.

populations at the conclusion of the experiment (44 months; Fig. S1). High precipitation significantly increased plant size for all populations beginning 14 months after the initiation of the precipitation treatment (Table S4; Fig. S1). Plants from all source populations responded similarly to watering (i.e., no significant population-by-precipitation interaction) until 44 months when we observed a significant population-by-precipitation interaction (Table 2c). Plasticity in growth (LRR effect size) was highly variable among populations; high precipitation (vs. low) increased the

growth of plants from the northern-most population (historically most stable precipitation environment) by 47% but increased growth by 181% in the southern population with the historically most variable precipitation environment (SM34; Fig. 2b). Precipitation variation at population sites predicted 86% of variation in plasticity in growth, whereas latitude was not significantly correlated with plasticity (Table S3; Fig. 3b).

Effects on flower production. There was not a significant main effect of source population on total flower production

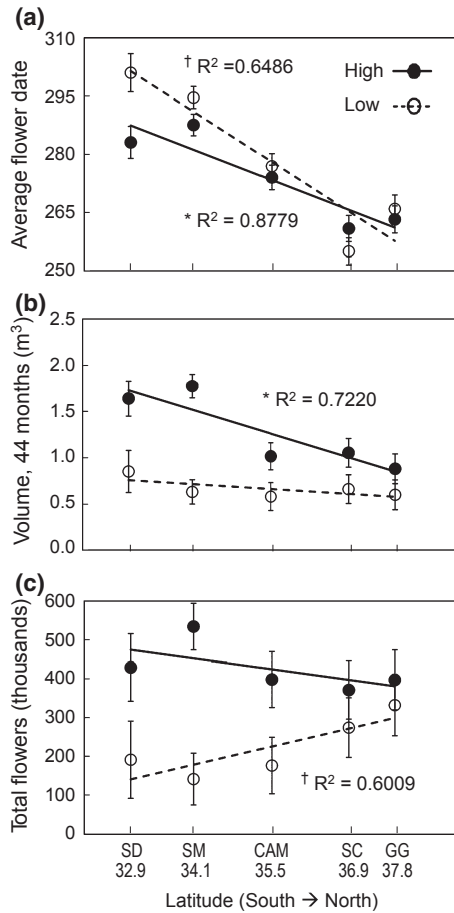


Fig. 2 Means \pm SE for plant performance (total growth and flower production) and phenology for five source populations grown under high and low precipitation conditions. Significant source population-by-precipitation interactions on plant performance and phenology indicate differences in plasticity between source populations. Regressions of source population means and latitude are shown separately for each treatment. Symbols next to R^2 values indicate the level of significance of the regression: $\dagger P < 0.05$, $*P < 0.05$, $**P < 0.01$.

across both precipitation treatments, but there was a significant population-by-precipitation interaction on flower production (Table 2c). Plasticity in flower production (LRR effect size) was highly variable among populations; high precipitation (vs. low) increased flower production of plants from the northern-most population (historically most stable precipitation environment) by 20% but increased flower production by 279% in the population with the historically most variable precipitation environment (SM34; Fig. 2c). Precipitation variation at population sites predicted 99% of variation in plasticity in flower production, whereas latitude was not significantly correlated with plasticity (Table S3; Fig. 3c).

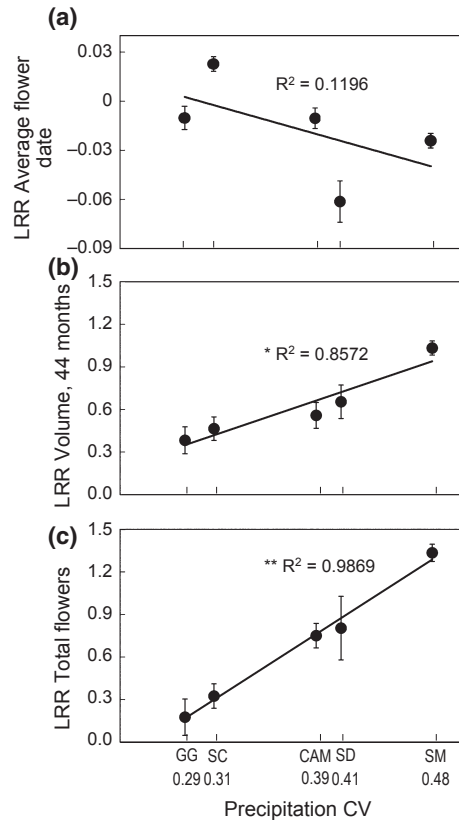


Fig. 3 Regressions of the log response ratio (response to increased precipitation) for plant performance and phenology and precipitation CV at each source population site indicate that variation in plasticity in plant performance tracks long-term environmental variation at source sites.

Accounting for type I error inflation

Our separate analysis of many plant responses (12 functional traits, 2 performance variables) by necessity increases the chance of type I error. Any conservative approach to α -adjustment (e.g., Bonferroni) results in very low statistical power (Garcia, 2004). Although excluding plant responses from our study would increase power, we reject this approach as it discards potentially important biological information. Our tests for the effects of source population, precipitation treatment, and their interaction yielded 8, 6, and 3 significant ($P < 0.05$) results, respectively. Based upon 14 statistical tests of each hypothesis, these numbers of significant outcomes are unlikely to occur by chance alone ($P = 8.6 \times 10^{-8}$, $P = 3.1 \times 10^{-5}$, and $P = 0.026$, respectively, based upon binomial expansion tests). Alternatively, P-plots can be used to infer the number of null hypotheses that should be rejected based upon the distribution of P values within a set of tests (Schweder & Spjøtvoll, 1982; Garcia, 2004). Our 14 tests for each hypothesis are expected to yield 8.9, 8.1, and 1.5

significant results, respectively. This approach suggests our conclusions for the main effects of population and precipitation can be safely accepted, but that our conclusions on their interactive effects carry a greater risk of type I error. Yet for two of the significant interactions (growth and flower production), follow-up analyses relating variation in precipitation effects to environmental variability were highly significant (Fig. 3, Table S3), thus providing strong independent support for these two conclusions as well.

Discussion

Examining clinal variation in both functional traits and plastic responses to an altered precipitation regime allows us to assess how contemporary patterns of adaptation to this steep environmental cline are likely to mediate future plant responses to projected climate change. We show that genetically based physiological, herbivore defense, and phenological traits and plant performance in *Artemisia californica* vary in concordance with a steep latitudinal cline in both the abiotic environment and environmental variability, suggesting clinal adaptation. Many plant traits were plastic, responding to increased precipitation in a manner that paralleled the genetically based trait differences observed between populations from wet and dry environments. Yet only for plant performance (growth, flowering) was there genetic variation in plasticity; there was strong, clinal variation in the strength of population responses to increased precipitation, and interannual variability in source site precipitation environment predicted nearly all of the variation in plasticity for both plant growth (86%) and flower production (99%). These strong clinal patterns of adaptation to both the environment and environmental variability indicate striking, yet predictable variation in the response of *A. californica* to the changes in precipitation predicted by most global change models. Furthermore, our analyses of climate data show that environmental variability may be increasing more in the north (historically stable environment) than the south (see Methods). If effects on plant performance (growth, flowering) are indicative of effects on population growth rate, these results suggest that *A. californica* populations experiencing the greatest change in environmental variability may be the least able to tolerate such change.

The clinal variation in performance and traits that we document here provides evidence of adaptation to this environmental gradient (Linhart & Grant, 1996). We found population variation in one measure of performance (growth) and 9 of 13 traits (%N, C : N, WUE, monoterpenes, sesquiterpenes, flowering duration,

average flower date [AFD], growth plasticity, flowering plasticity) and for seven of these traits (including plasticity), the variation was clinal. Interestingly, across precipitation treatments there was not a cline in flower production although there were opposing clines in the number of inflorescences (decreasing northward) and flowers per inflorescence (increasing northward). The especially steep gradient (fourfold variation) in precipitation, and the concordance between clinal population variation in traits and trait responses to our precipitation manipulation suggest that precipitation is a key selective factor. In addition, for all clinally varying traits either precipitation or latitude (the latter representing precipitation in combination with other factors) explain much of this variation (i.e., high R^2), whereas only for WUE was there an association with temperature. In terms of plasticity, southern populations from more arid and variable environments showed higher levels of plasticity in growth and flower production in response to water. This plasticity was best explained by precipitation CV, which is the only measure of variation that is clinal across this gradient, thus supporting predictions that interannual environmental variation contributes to the evolution of plasticity in such variable environments (Bradshaw, 1965; Sultan, 2000; Balaguer *et al.*, 2001). In a Mediterranean environment, the ability to utilize water opportunistically is likely selected for particularly in more arid and variable regions thus allowing populations from such environments to maximize growth and/or fitness under favorable conditions (Grant *et al.*, 2005). In similar studies, Gianoli (2004) found that populations of *Convolvulus arvensis* from more heterogeneous moisture environments were more plastic in growth but not in reproductive traits, and Grant *et al.* (2005) found variation in plasticity in growth characteristics (e.g., number of leaves, branch length) among populations of the Mediterranean shrub *Cistus albidus* in response to a precipitation manipulation. Although these and other studies have examined intraspecific variation in plasticity among plant populations (Sultan & Bazzaz, 1993; Volis *et al.*, 2002; Heschel *et al.*, 2004), quantitative measures of environmental variation and explicit tests of relationships between plasticity and variation in specific environmental variables have rarely been incorporated into analyses (Gianoli, 2004).

The clinal patterns and responses to precipitation in plant morphological and physiological traits that we observed are generally in accordance with patterns of intraspecific genetically based variation documented in other common garden studies, whereas our results for flowering phenology give mixed support. Other studies have similarly found that whereas PWC and SLA respond plastically to increased water, these traits do

not often show genetically based variation among populations (e.g., Gianoli, 2004; Woods *et al.*, 2012; but see Etterson & Shaw, 2001; Scheepens *et al.*, 2010). Although we did not find population or treatment variation in predawn and mid-day water potentials (ψ_{Pd} and ψ_{Md}), we measured water potential at least 72 h after precipitation events, thus quantifying longer term effects of precipitation on plant-water relations, not transient effects (Grant *et al.*, 2005). In contrast, the pattern of clinal variation in WUE was unexpected (Larcher, 2003), as southern populations (from more arid environments) had lower WUE than northern populations (from more mesic environments). We suspect southern plants were not fully water-stressed in the common garden environment and may be adjusting other physiological traits linked to plant-water relations (e.g., leaf absorptance, stomatal conductance, transpiration rates), resulting in lower realized WUE (Roy & Mooney, 1982; Farquhar *et al.*, 1989; Sandquist & Ehleringer, 1997). Although arid habitats can select for earlier reproduction as an adaptation to avoid the potential early onset of seasonal drought (Jonas & Geber, 1999; Gianoli, 2004; but see Woods *et al.*, 2012), *A. californica* showed the reverse, with southern populations flowering later. This may be due to the seasonal timing of flowering for *A. californica*, which begins during the seasonally dry summer and peaks after the onset of the fall rainy season. We also observed non-clinal variation in plasticity for flowering time with the two southernmost populations, SD33 and SM34, shifting flowering earlier in response to added precipitation, and one northern population (SC37) shifting flowering later.

It has been broadly suggested that biotic interactions such as herbivory are more important at lower latitudes and select for greater levels of plant defense (Dobzhansky, 1950) yet empirical evidence is mixed both for interspecific (Coley & Aide, 1991; Schemske *et al.*, 2009; Moles *et al.*, 2011) and intraspecific comparisons (Salgado & Pennings, 2005; Pennings *et al.*, 2009; Woods *et al.*, 2012). Our results are consistent with predictions for southward increases in herbivore defense and decreases in plant quality, with southern populations having higher concentrations of monoterpenes (a trend, $P = 0.0911$), lower percent N, and higher C : N. Although tradeoffs between plant growth and defense are predicted and observed both among (Coley *et al.*, 1985; Fine *et al.*, 2004; Mooney *et al.*, 2010) and within species (Donaldson *et al.*, 2006; Sampedro *et al.*, 2011), we found no evidence of such tradeoffs; plants from southern populations had faster growth rates and were better defended than northern plants. Plant adaptation to the abiotic and biotic environment is likely to be deeply intertwined and the clines that we observe may be

driven by southward aridity (e.g., not seen in Salgado & Pennings, 2005; Pennings *et al.*, 2009; Woods *et al.*, 2012), and we do not know if there is geographic variation in herbivory across this gradient, which is the basis of these predicted patterns and tradeoffs (Dobzhansky, 1950; Coley *et al.*, 1985; Schemske *et al.*, 2009). It is also possible that such tradeoffs are environment dependent and would be evident if the experiment were performed at sites with different abiotic or biotic conditions than those of our common garden site.

The apparent adaptation to clines in precipitation and temperature that we document here suggests that changes in these parameters have the potential to alter selection. The effects of climate change and subsequent changes in the selective environment on plant performance are likely to differ among populations. In particular, increased precipitation variability can reduce water availability (Sher *et al.*, 2004; Knapp *et al.*, 2008) and influence plant stress and productivity (Fay *et al.*, 2002; Sher *et al.*, 2004). For *A. californica*, such a shift in climatology is likely to increase drought stress (Sher *et al.*, 2004; Knapp *et al.*, 2008); such water stress is known to be a particularly strong selective force in arid and semi-arid ecosystems (Niklas, 1997). In addition, consequences of climate change may be exacerbated by *A. californica*'s long generation time, reduced gene flow due to habitat fragmentation (Davis *et al.*, 1994; Vandergast *et al.*, 2007), and interactions between the effects of altered climate and other drivers of global change such as fire (Keeley *et al.*, 2005), invasive species (Talluto & Suding, 2008), and nitrogen deposition (Bytnerowicz & Fenn, 1996; Fenn *et al.*, 2010). For long-lived plants, insufficient rates of natural seed dispersal coupled with genetic constraints on adaptation, are likely to reduce the rates of migration and adaptation well below the pace required with respect to climate change (Davis & Shaw, 2001).

The predicted increases in interannual precipitation variation for California, and globally (Easterling, 2000; Weltzin *et al.*, 2003; Meehl *et al.*, 2007), are likely to have different impacts across the range of *A. californica*. The historically variable environments of the south support locally adapted genotypes that may be better suited to projected increases in variability than those adapted to northern, historically stable environments. Furthermore, our analyses of climate data (see Methods) show nonuniform increases in precipitation variation across the range of *A. californica* with 4% average increases in interannual CV for southern-most populations and 29% average increases for northern-most populations (pre- vs. post-1980). Accordingly, those northern populations adapted to the most stable environment, and with the lowest levels of plasticity, may be increasing in precipitation variability the most.

In conclusion, this study illustrates the value of incorporating past and projected environmental variability into the study of plant phenotypic variation. In particular, understanding historical environmental variability, and adaptation to it, is likely critical to anticipating future responses to global change. From a management standpoint, restoration practitioners should assess and consider the plasticity of plant material used in restoration and in this instance, using a mixture of local and nonlocal genotypes at northern latitudes could ensure some tolerance to change in restored populations and increase gene flow across the range. In addition, our data indicate that there may be ecologically important and predictable intraspecific variation in a species' ability to respond to environmental change that could be incorporated into climate models. Our findings point to the critical need for conceptual frameworks that incorporate biological processes such as local adaptation and adaptive plasticity into forecasts of ecosystem response to future climates.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix A. Methods and results of Principal Components Analysis performed on *A. californica* functional traits and performance.

Table S1. Location and climate data summaries of 24 coastal California weather stations used for analyses of latitudinal patterns.

Table S2. Variances and pairwise Pearson correlation coefficients for all measured plant traits and performance (growth, flowering) of *Artemisia californica*.

Table S3. Statistics for regressions between population means and latitude, precipitation and temperature for plant traits with significant source population effects.

Table S4. Statistics for main and interactive effects of source population and precipitation treatment on *A. californica* volume over time.

Figure S1. Plant volume (means \pm SE) over time ($N = 8$ measurements; see Table S4 for dates) for five source populations grown under high and low precipitation in common garden plots.