Annual plants change in size over a century of observations

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Abstract

Studies have documented changes in animal body sizes over the last century, but very little is known about changes in plant sizes, even though reduced plant productivity is potentially responsible for declines in size of other organisms. Here, I ask whether warming trends in the Great Basin have affected plant size by measuring specimens preserved on herbarium sheets collected between 1893 and 2011. I asked how maximum and minimum temperatures, precipitation, and the Pacific Decadal Oscillation (PDO) in the year of collection affected plant height, leaf size, and flower number, and asked whether changes in climate resulted in decreasing sizes for seven annual forbs. Species had contrasting responses to climate factors, and would not necessarily be expected to respond in parallel to climatic shifts. There were generally positive relationships between plant size and increased minimum and maximum temperatures, which would have been predicted to lead to small increases in plant sizes over the observation period. While one species increased in size and flower number over the observation period, five of the seven species decreased in plant height, four of these decreased in leaf size, and one species also decreased in flower production. One species showed no change. The mechanisms behind these size changes are unknown, and the limited data available on these species (germination timing, area of occupancy, relative abundance) did not explain why some species shrank while others grew or did not change in size over time. These results show that multiple annual forbs are decreasing in size, but that even within the same functional group, species may have contrasting responses to similar environmental stimuli. Changes in plant size could have cascading effects on other members of these communities, and differential responses to directional change may change the composition of plant communities over time.

Keywords: Blepharipappus scaber, climate change, *Collinsia parvitlora*, *Cryptantha pterocarya*, disturbance, *Eriastrum signatum*, evolution, *Gilia inconspicua*, *Mentzelia albicaulis*, *Microsteris gracilis*, plasticity

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Introduction

Resource availability can affect the evolution of organism size in both plants and animals, with larger plants dominating areas with mesic climates such as temperate and tropical forests, and smaller statured plants dominating warmer, drier areas such as grasslands, savannahs, and deserts (Woodward & Williams, 1987). In addition, animal mass displays latitudinal clines within and across species in response to large-scale environmental shifts (James, 1970; Blackburn *et al.*, 1999; Ashton *et al.*, 2000; Meiri & Dayan, 2003), and both animals and plants change in size on islands relative to mainlands, presumably in response to differences in resource availability (Burns *et al.*, 2012; Lomolino *et al.*, 2012).

Shifts in the average size of organisms can also occur in a single location that undergoes changes in resource availability. For example, middens provide evidence that woodrat body size decreased during the most recent transition from glacial to interglacial period (Smith *et al.*, 1995). Strong negative correlations between tree ring size and increased temperatures have been observed in white spruce trees in Alaska, resulting in decreased ring size over time as the climate in this region becomes increasingly warmer (Barber *et al.*, 2000). These changes are not isolated events: recent reviews of organism size shifts over the past two decades provide many examples of size increases and decreases in birds, mammals, and ectotherms (Gardner *et al.*, 2011). Sheridan & Bickford (2011) also reviewed studies of changing size and report 38 examples of size decreases, 9 examples of size increases, and 38 examples of no size changes. Hypothesized causes of decreased size include reductions in resource availability due to climate change as well as physiological responses to increasing temperatures (Gardner *et al.*, 2011).

Plants are a major component of terrestrial biomass, and are likely to be directly or indirectly responsible for changes in resource availability for birds, mammals,

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and other animals, but there are limited studies of directional changes in plant size in response to changing climates. Among these are the previously mentioned study of white spruce (Barber *et al.*, 2000), a study documenting decreases in leaf thickness of the shrub *Dodonaea viscosa* subsp. *angustissima* over 127 years in Australia, presumably in response to warming (Guerin *et al.*, 2012), and changes in flowering phenology and size at flowering in response to selection imposed by a 5-year drought (Franks & Weis, 2008).

Causes of these shifts in size are either phenotypically plastic responses to environmental change, changes in gene frequency, or both. The ability of plants to respond in phenotypically plastic ways to resource availability is well documented (Schlichting, 1986), but plant size can also evolve in response to directional changes in their environment. In the Great Basin of the western United States, where invasion of the highly competitive *Bromus tectorum* L. has resulted in the reduction in soil resources for native plants, I have observed evidence for the evolution of decreased size in native species growing in *B. tectorum*-invaded sites (Leger, 2008; Rowe & Leger, 2011), and found that smaller statured plants survived better than larger ones when seeded into invaded sites (Kulpa & Leger, 2013). Evidence from agricultural (Blum & Sullivan, 1997; Angadi & Entz, 2002) and natural (Hendrix *et al.*, 1991; Hendrix & Trapp, 1992; Casper, 1996) systems supports the idea that small size can be adaptive under drought conditions, as smaller plants transpire less than larger ones and can survive with reduced resources. It is possible to differentiate between evolutionary and plastic causes of observed shifts in size for studies of short-term change (e.g., Franks & Weis, 2008). Determining whether there are genetic causes of observed change is more difficult for longer term studies, as organisms cannot be reared in common environments and a lack of knowledge of specific genes that affect organism size precludes the use of molecular methods to detect changes in gene frequency over time (but see Umina *et al.*, 2005), thus the degree to which genetic change is responsible for size shifts is mostly unknown.

Herbarium specimens have been used to measure changes in plant flowering phenology (Primack *et al.*, 2004; Miller-Rushing *et al.*, 2006) and leaf morphology (Guerin *et al.*, 2012) in response to climate change, and decreases in plant size due to human harvest (McGraw, 2001; Law & Salick, 2005), but have not been used to investigate changes in size and reproductive output in response to climate change. Using herbarium records from over a century of collections and climate data from the year of plant collection, I asked how interannual variation in climate affected plant size for annual forbs in the Great Basin, considering results in light of differences in germination timing, distribution, and abundance among species, and, given climate change, asked whether there has been a long-term trend in plant size and reproductive output. I predicted that global climate factors (e.g., the Pacific Decadal Oscillation) as well as regional-scale factors would affect plant size, and expected to see larger annual plants in years with greater water availability during the growth season, as desert plants are strongly affected by water availability and temperature at the time of precipitation (Noy-Meir, 1973; Smith *et al.*, 1997). Although species-specific responses to variation in temperature and precipitation are common in annual species (e.g., Robinson & Gross, 2010; Kimball *et al.*, 2012), I expected most species to be larger during years with warmer falls and winters (which would allow for more plant growth during the seasons with highest water availability), cooler springs and summers, and higher precipitation. I expected overall plant sizes to decrease as a result of warming spring and summer temperatures, which would increase drought stress for annual plants growing in these desert systems.

Materials and methods

I selected seven small-statured annual plants common to semi-arid ecosystems of the Great Basin–Mojave Desert floristic province of the western United States. I chose to use small-statured plants because they would be less likely to suffer from collector bias, which may occur if collectors are choosing small individuals from a population to fit them on a 41.9 × 26.7 cm herbarium sheet. I chose to study annual, rather than perennial, species because their performance can be linked more closely to growing conditions in a single year. Species surveyed were as follows: *Blepharipappus scaber* Hook. (Asteraceae), *Collinsia parviflora* Lindl. (Plantaginaceae), *Cryptantha pterocarya* (Torr.) Greene (Boraginaceae), *Eriastrum signatum* D. Gowen (Polemoniaceae), *Gilia inconspicua* (Sm.) Sweet (Polemoniaceae), *Mentzelia albicaulis* (Hook.) Torr. & A. Gray (Loasaceae), and *Microsteris gracilis* (Hook.) Greene (Polemoniaceae), chosen because they are common annual forbs I have observed growing in the Great Basin that had sufficient representation (at least 30 collections) available for measurements. Relatively little is known about the ecology of annual forbs in the cold desert, but as a group, desert annual forbs can be most common in communities after disturbance, with specific observations of *Eriastrum* occurring after wildfires (Prater *et al.*, 2006), *M. gracilis* occurring in recently disturbed soils (Brandt & Rickard, 1994) and after fires (Humphrey, 1984). *Mentzelia albicaulis* and *C. pterocarya* were among the most successful colonizers in disturbed areas of the Nevada Test Site (Rickard & Shields, 1963). Of these seven species, *C. parviflora* is the best studied, but primarily as a system for studying mating systems and plant/pollinator interactions (e.g., Kennedy & Elle, 2008).

The timing and temperature during precipitation events in western deserts has led to the evolution of two main strategies among annual plants. Winter annuals emerge in the fall and overwinter as small rosettes, whereas spring annuals delay germination until later in the season, emerging when soil temperatures and moisture are more favorable (Baskin & Baskin, 2001). The seed ecology of *E. signatum, M. albicaulis*, and *B. scaber* is consistent with spring germination, as seeds require a prolonged cold, wet stratification before germination (Forbis, 2010), and *M. gracilis* has the ability to germinate in either the winter or the spring (Guerrant & Raven, 1995). *Collinsia parviflora* and *Cryptantha pterocarya* are considered winter annuals, germinating without need of extended cold stratification (*C. parviflora*, Kennedy & Elle, 2008; *C. pterocarya*, E.A. Leger, unpublished results) and the germination preferences of *G. inconspicua* are unknown (Table 1).

I categorized the distribution of each species by tabulating the percent occupancy of counties in western US states in general, and in Nevada in particular, which is the western state that is most dominated by the Great Basin–Mojave Desert floristic province, using the Biota of North America Program (Kartesz, 2011). This measure is almost certainly an overestimate of the area of occupancy, as a county is considered 'occupied' if the plant occurs anywhere within the boundary, but it provides a relative measure of the overall range of each species. To estimate plant abundance, I queried the number of collections for each species from the Consortium of Intermountain Herbaria (http//:inter-mountainbiota.org/portal/index.php), a collection of online specimen information from over 40 herbaria (Table 1). These collections may be biased toward particularly apparent species or species of particular interest, but as these seven forbs are all diminutive and not well studied, these data likely provide general information on relative abundance in the wild. Taken together, these statistics suggest that some of these species are both widespread and abundant (*C. parviflora, M. albicaulis*), as they have large areas of occupancy and are commonly collected, while one species, *B. scaber*, has a restricted distribution and was collected relatively infrequently. The remaining species, *M. gracilis, C. pterocarya, G. inconspicua*, and *E. signatum*, listed in decreasing order of area of occupancy and collection frequency, are found throughout most of Nevada (Table 1).

Measurements were taken from plants collected from Nevada housed in the University of Nevada, Reno (UNR) herbarium. This herbarium contains specimens collected from surveys that began in 1893 and holds the most extensive collections from the 1930s and 1970s (Fig. 1). In addition to the specimens from the UNR herbarium, digital scans of collections from Nevada were available for some species from the New York Botanic Garden, and UNR's collections were supplemented with some digital sheets. Numbers of individuals per sheet ranged from 1 to 22 individuals, with averages of 3–7 plants per sheet (Table 1); in total, 1940 individual plants were measured from 406 herbarium sheets. Collection periods for all species spanned more than 100 years (Table 1). Six species had collections well dispersed throughout the sampling period, but one species, *G. inconspicua*, had very limited sampling before the 1970s, with only one collection in 1893. Some sheets, especially older specimens, lacked specific elevation,

Table 1 Annual forb species included in this study, with plant family and germination timing, if known. Regional abundance and occupancy are shown, including the percent occupancy of counties in all western states and Nevada, and the number of herbarium sheets present for each species in other intermountain herbaria. The number of sheets sampled in this study from the UNR herbarium is shown for each species, followed by the total number of plants measured, as well as the range of collection period, number of plants per sheet (average and SE), and the median height per sheet (with SE) of plants used for this analysis

Species	Family	Germination timing	% Occupancy of western counties*	% Occupancy in NV†	# Sheets, regional‡	# Sheets, # plants	Date range	Plants per sheet	Median height (cm)
Blepharipappus scaber	Asteraceae	Spring	12.8	23.5	49	36, 111	1907–2008	3.1 (0.3)	16.5 (0.9)
Collinsia parviflora	Plantaginaceae	Winter	70.3	100.0	1686	93, 592	1901–2005	6.4 (0.5)	8.2 (0.5)
Cryptantha pterocarya	Boraginaceae	Winter	26.8	94.1	1531	98, 434	1893–2005	4.5 (0.4)	17.4 (0.8)
Eriastrum signatum	Polemoniaceae	Spring	14.5§	82.4§	216	30, 125	1893–2008	4.2 (0.6)	13.5 (1.0)
Gilia inconspicua	Polemoniaceae	Unknown	16.4	88.2	648	30, 131	1893–2011	4.4 (0.7)	16.2 (1.4)
Mentzelia albicaulis	Loasaceae	Spring	52.7	100.0	1460	65, 192	1901–2005	3.0 (0.3)	21.0 (1.7)
Microsteris gracilis	Polemoniaceae	Both	73.7	94.1	939	54, 355	1894–2005	6.6 (0.6)	5.3 (0.4)

*Percentage of 414 counties occupied in 10 western states: AZ, CA, CO, ID, MT, NM, NV, OR, WA, WY.
†Percentage of 16 counties in NV occupied. Data from Kartesz, 2011.
‡Number of collections in the Intermountain Region Herbarium Network, a consortium of over 40 herbaria in western states; does not include the UNR (University of Nevada, Reno) herbarium records.
§Occupancy data presented from combined records of *Eriastrum sparsiflorum* and *E. signatum* due to taxonomic changes not reflected in older regional floras.
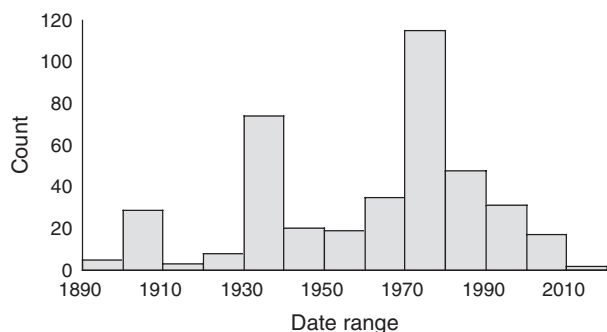
Fig. 1 Distribution of collection dates from herbarium specimens of seven annual forbs in Nevada. Collections used in this study are housed primarily at the University of Nevada, Reno herbarium, with supplemental samples from the digital collection at the New York Botanical Garden.

latitude, or longitude values. When possible, this information was inferred from descriptions of collection locations using the United States Geologial Survey (USGS) Geographic Names Information Finder (http://geonames.usgs.gov), expert opinion of the herbarium curator, and maps. Specimens with insufficient information to identify a collection location were not included in this analysis. Although individual plants on a sheet are not independent samples, analyses were conducted on individual plant data, rather than on sheet means, to maintain larger sample sizes.

Plant height was measured by recording the length of the plant from the top of the plant to the start of the root, using a string to measure height on curved or folded specimens, and the program AnalyzingDigitalImages (http://www.global-systemsscience.org/software) was used to measure sizes of digital specimens. The phenological stage (whether a plant was in fruit, in flower, neither, or both), the length of the lowest true leaf, and the number of flowers, fruits, and flower buds per plant were recorded for each plant, as was the date of collection (days since January 1). These plants can have a flowering period of many months (early spring through summer), and collection date positively affected plant size (data not shown), so this variable, which approximates plant age, was included as a covariate in analyses. Similarly, plant phenological stage affected plant size, with plants in fruit significantly larger than plants with both fruit and flowers, which were, in turn, significantly larger than plants with flowers but no fruit or vegetative plants (data not shown), and thus phenological stage of each was also included in analyses.

Weather data were gathered from the PRISM Climate Group (http://prism.oregonstate.edu), using information from the collection location closest to the center of the collection range of each individual species. Average maximum and minimum temperatures were calculated for fall through winter (fall/winter) and spring through summer (spring/summer) and annual precipitation was summed for the 12-month period that spanned the growing season for each sheet (September–December of the year prior to collection, and January–August of the year of collection). PRISM climate data are available from 1896 onward, and thus five sheets collected in

1893 and 1894 were excluded from analyses that included climatic variables. Longer term climate trends, measured by the average Pacific Decadal Oscillation (PDO, http://jisao.washington.edu/pdo/PDO.latest) during the growing year, were also included in analysis. Changes in climate in the general collection region over time were analyzed with linear regression between years (1896 to 2011) using the maximum and minimum seasonal temperatures and precipitation values averaged from all species.

The effect of climatic variables on plant height and flower number was analyzed using a three-step process. First, to control for plant age and phenology, linear models were run with these two factors and plant height and flower number as dependent variables, and residuals were saved. Second, model averaging was used separately for height and flower number residuals to identify the factors with the strongest effects, estimated with maximum likelihood, averaged across all possible models with a maximum of eight factors (limited to eight to reduce computational intensity). Candidate variables included year, elevation, latitude, longitude, fall/winter and spring/summer maximum and minimum temperatures, annual precipitation, and PDO. A subset of these variables was selected for further analysis based on parameter estimates that were significantly different from zero (i.e., the SE of coefficients derived from standardized variables did not overlap zero) after model averaging. Finally, this subset of factors was used in multiple regression models with both height and flower residuals as dependent variables. To avoid multicolinearity, factors with variance inflation factors >3 were eliminated from the model. Significance was determined using the false discovery rate method (Benjamini & Hochberg, 1995) to reduce the likelihood of Type I error. Throughout the analyses, temperature and precipitation data and response variables were standardized to a mean of 0 and SD of 1 to allow comparisons of relative effect sizes between variables and among species.

To test for long-term trends, ANCOVA was used to determine if there were changes in plant height, leaf size, and flower production over time. Although year was a factor initially included in the previous analysis, it was sometimes removed from final models to reduce colinearity. This second analysis included the continuous variables year, elevation, latitude, longitude, collection date, and the categorical variable of plant phenological stage as model factors, and plant height, leaf size, and flower number as model responses in separate models. To determine if changes in plant size over time were related to abundance and distribution, correlations were conducted between the number of collections in all regional herbaria and the two different percent occupancy measures and the slope of the regression line between year and plant size. ANOVA was used to compare the slopes of the regression lines for the three known spring annuals and the two winter annuals.

Response variables were log transformed as required to meet the assumptions of normality of residuals and homogeneity of variances for ANOVA (transformations indicated in Table 3). Analyses were conducted using JMP 10.0.0 (SAS Institute Inc., Cary, NC, USA).

Results

Climate change

Minimum and maximum temperatures rose significantly between 1896 and 2011 across the collection area (Fig. 2a). The largest increases were observed in fall/winter minimum temperatures (1.8 °C increase), followed by spring/summer maximum temperature (1.6 °C), spring/summer minimum (1.6 °C), and fall/winter maximum temperatures (0.9 °C). Annual precipitation did not show directional change over time (Fig. 2b, $P = 0.2172$), maintaining an annual average of 276 mm throughout the study period, and the PDO cycled between positive, warmer values and negative, cooler/wetter patterns with no linear change over time (Fig. 2c, $P = 0.6939$).

Plant responses to climate

Species had individualized size responses to specific climatic factors, with no two species responding in exact parallel (Table 2). Some commonalities were observed, however, in mostly positive plant height responses to increasing minimum temperatures, and all but one species, E. signatum, was taller in years with increased minimum temperatures in either spring/summer (five species) or fall/winter (two species, Table 2a). Height responses to increased maximum temperatures in fall/winter were significantly positive for C. parviflora and M. gracilis, and G. inconspicua was taller in response to increased spring/summer maximum temperatures. In contrast, M. albicaulis and M. gracilis were shorter in

spring/summers with increased maximum temperatures (Table 2a). Increased annual precipitation only affected two species, leading to increased height in B. scaber and decreased height in M. albicaulis (Table 2a). Gilia inconspicua and M. gracilis responded positively to warmer PDO cycles, whereas C. parviflora performed better in years with cooler cycles (Table 2a). Location also affected plant size, with elevation or longitude explaining a significant amount of size variation in five species (elevation: B. scaber, C. parviflora, and G. intermedia; longitude: C. pterocarya, G. intermedia, and M. gracilis).

Flower number also responded to climatic factors in species-specific ways, and factors that affected flowering were sometimes different from those that affected plant size. Warmer minimum and maximum temperatures were associated with increased flower production for five species. Three species, C. parviflora, E. signatum, M. gracilis, increased their flower number in years with warmer fall and winter minimum temperatures, whereas B. scaber increased flower production in response to warmer fall/winter minimum temperatures (Table 2b). Eriastrum signatum, G. inconspicua, and M. gracilis increased flower production in years with warmer fall/winter maximum temperatures. Eriastrum signatum and M. gracilis were the only species to significantly decrease flower production in response to warming, in response to increased spring/summer maximum and fall/winter minimum temperatures, respectively. Flower production responses to increased annual precipitation were mixed, with increased flower number in two species and decreased flower production in two others (Table 2b). Paralleling height responses, G. inconspic-
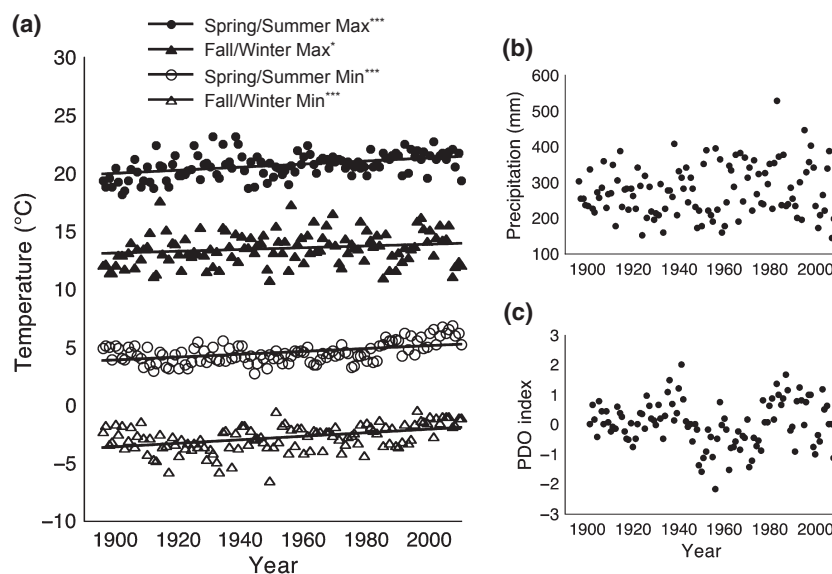

Fig. 2 Changes in fall/winter, spring/summer maximum and minimum temperatures (a) and total annual precipitation, (b) averaged from the center of the collection range for all species, and the Pacific Decadal Oscillation (PDO), and (c) Regression lines are fit to significant relationships, and asterisks indicate significance level: *$P < 0.05$, ***$P < 0.0001$.

Table 2 Standardized beta coefficients for plant height (a) and flower number (b) from multiple regression models testing the impact of climate variables on plant performance. Bold values indicate significance, blue indicates positive responses, and red indicates negative responses. Italicized values are significant relationships that would be expected to result in reduced plant height or flower production, given the direction of climate change since 1896

	BLSC	COPA	CRPT	ERSI	GIIN	MEAL	MIGR
(a) Plant height							
Fall/winter min. temp.	–	**0.14***	–	–	**0.26***	–	–
Spring/summer min. temp.	**0.21***	**0.19****	**0.17***	−0.09	–	**3.8*****	**0.28*****
Fall/winter max. temp.	–	**0.22****	–	0.20	0.02	−0.96	**0.26*****
Spring/summer max. temp.	–	–	–	−0.19	**0.24***	**−3.3***	**−0.23*****
Annual precipitation	**0.32***	–	–	−0.26	−0.14	**−2.85****	–
PDO	–	**−0.12***	0.10	0.23	**0.45*****	–	**0.14***
(b) Flower number							
Fall/winter min. temp.	**0.43*****	0.10	–	–	–	–	**−0.28*****
Spring/summer min. temp.	–	**0.13***	–	**0.47*****	–	−0.13	**0.32*****
Fall/winter max. temp.	–	–	−0.03	**0.40*****	**0.30***	–	**0.44*****
Spring/summer max. temp.	–	–	–	**−0.26***	−0.16	–	–
Annual precipitation	**0.18***	**−0.11***	−0.14	**−0.25***	−0.21	**−0.20***	–
PDO	–	–	–	–	**0.32***	**−0.25***	**0.24*****

P value criteria for significance adjusted by the method of Benjamini & Hochberg (1995); *$P < 0.032$ in A; *$P < 0.035$ in B; **$P < 0.001$; ***$P < 0.0001$.
PDO, Pacific Decadal Oscillation; BLSC, *Blepharipappus scaber*; COPA, *Collinsia parviflora*; CRPT, *Cryptantha pterocarya*; ERSI, *Eriastrum signatum*; GIIN, *Gilia inconspicua*; MEAL, *Mentzelia albicaulis*; MIGR, *Microsteris gracilis*.

ua and *M. gracilis* increased flower production in years with warmer PDO cycles, whereas *M. albicaulis* had the opposite response. Location also affected flower production, with elevation and longitude as factors explaining a significant amount of variation in four species (elevation: *B. scaber*, *E. sparsiflorum*; longitude: *E. sparsiflorum*, *G. intermedia*, and *M. gracilis*).

Only two species showed relationships with environmental factors that would be expected to lead to decreases in height due to climate change (*M. albicaulis* and *M. gracilis* responded negatively to warmer spring/summer maximum temperatures), but these species also had relationships with changing climate variables that would be expected to have positive effects on height (i.e., positive responses to increased minimum spring/summer temperatures for both species, and to increased fall/winter maximums for *M. gracilis*). Flower number might be predicted to decrease for *E. signatum* and *M. gracilis* in response to increases in maximum spring/summer and minimum fall/winter temperatures, respectively, but both of these species also had strong positive responses to two different elements of climate change, namely increased spring/summer minimum and fall/winter maximum temperatures.

Changes in plant size and reproduction

Five of seven annual forb species (*C. parviflora*, *C. pterocarya*, *E. signatum*, *M. gracilis*, and *G. inconspicua*)

decreased significantly in height over time (Table 3, Fig. 3), and of these five, all but *G. inconspicua* also decreased in average leaf size (Table 3). Decreases in height ranged from 0.023 to 0.056 cm yr^{-1} over the observation period (Fig. 3). Only one species, *C. pterocarya*, decreased flower production in addition to decreasing in height and leaf size. One species, *M. albicaulis*, increased significantly in height and flower number, and one species, *B. scaber*, did not change over time (Table 3, Fig. 3).

The degree and direction of change in size over time was not related to the number of collections in regional herbaria (Pearson $r = 0.37$, $P = 0.4182$) or area of occupancy, at either the scale of western states (Pearson $r = 0.49$, $P = 0.2652$) or in Nevada alone (Pearson $r = 0.07$, $P = 0.8774$). There was no relationship between the degree of change in size over time and timing of seed germination ($F_{1,3} = 0.43$, $P = 0.5572$), as the three known spring germinators showed no change (*B. scaber*), significant size decreases (*E. sparsiflorum*), or significant size increases (*M. albicaulis*) over the observation period.

Discussion

Plants can readily change their size and reproductive output, displaying a high degree of phenotypic plasticity in response to resource availability (Pigliucci, 2001). In warming experiments, plants have been observed to

Table 3 Results for one factor, collection year, from an ANCOVA that included collection year, elevation, latitude, longitude, collection day, and plant phenology. Reponses are plant height, flower number, and length of the lowest true leaf for seven annual forbs. Values are F ratios with numerator df, denominator df presented in subscript (top row); P values (bottom row) are bolded when significant

	BLSC	COPA	CRPT	ERSI	GIIN	MEAL	MIGR
Direction of change†	–	Decreasing	Decreasing	Decreasing	Decreasing	Increasing	Decreasing
Height	$1.7_{1,65}$	$21.6_{1,434}$	$12.3_{1,306}$	$9.8_{1,119}$	$4.2_{1,124}$	$12.5_{1,183}$	$29.2_{1,348}$
	0.1983*	**<0.0001***	**0.0005**	**0.0022**	**0.0431**	**0.0005**	**<0.0001***
Flower #	$1.9_{1,65}$	$0.02_{1,433}$	$11.0_{1,303}$	$3.0_{1,119}$	$0.04_{1,124}$	$21.4_{1,183}$	$2.6_{1,348}$
	0.1680*	0.9003	**0.0010***	0.0848*	0.8316*	**<0.0001**	0.1085*
Leaf length	$0.007_{1,64}$	$16.5_{1,434}$	$9.2_{1,273}$	$4.7_{1,119}$	$0.8_{1,124}$	$3.3_{1,183}$	$67.6_{1,348}$
	0.9295	**<0.0001**	**0.0025**	**0.0324**	0.3643	0.0712	**<0.0001**

BLSC, *Blepharipappus scaber;* COPA, *Collinsia parviflora;* CRPT, *Cryptantha pterocarya;* ERSI, *Eriastrum signatum;* GIIN, *Gilia inconspicua;* MEAL, *Mentzelia albicaulis;* MIGR, *Microsteris gracilis.*
*Indicates variable was log transformed for analysis.
†Direction of change for variables showing significant change over time.

reduce above-ground biomass by 3–17% for every 1 °C temperature increase, presumably as a result of water limitation (Sheridan & Bickford, 2011). In a warming world, we might expect individual plants to decrease in size just as animals have been observed to do (Gardner *et al.*, 2011; Sheridan & Bickford, 2011), either as a direct response to water limitation or, in some cases, in response to soil nutrient loss from increased fire frequency (e.g., Vitousek *et al.*, 1982; Blank *et al.*, 1994). In this study, I observed the predicted shrinking response in five of seven annual forb species, with four of these species also showing reductions in leaf size. One species increased in height and leaf size, while another showed no change over time. Maximum and minimum temperatures increased significantly over the study period, but size decreases were not, as expected, due to negative correlations with increasing temperatures. Instead, over the survey period, six of these annual forbs were largest in years with increased minimum temperatures, and four species had positive responses to increased fall/winter maximum temperatures. I predicted that plants would be smaller in years with higher spring/summer maximum temperatures, but this was only true for two species, one of which actually increased in size over time (*M. albicaulis*). Although increased temperatures without changes in precipitation might be expected to lead to water deficits for these annuals, a pattern which has been seen in other desert species (Weltzin *et al.*, 2003), this does not appear to have been the case for most of these annuals during this study period, indicating that these temperature increases may be within the range of tolerance for most of these species.

Despite divergent preferences for growing season variables, reductions in size were still seen as a common response over time from five species. In addition,

there were no obvious climate preferences in common between the two species that did not shrink, as they had similar responses to most climate variable as the other species, differing only in that these two species were the only ones with sizes affected by annual precipitation, although in different directions (Table 2). Thus, other ecological factors may explain declines in plant size for some species, but not others, such as the ability to respond plastically to environmental cues or the ability to tolerate low resource conditions, which have been linked to differential responses to variation in temperature and precipitation in other desert annual species (e.g., Kimball *et al.*, 2012). One might have expected climate warming to affect spring-germinating species more than winter annuals, as warming in the spring months might be more stressful for seedlings than for juvenile plants, but this was not the case.

Area of occupancy has been linked to ecological traits, such as a positive association with colonization ability (e.g., Leger & Forister, 2009), and has been hypothesized to be related to niche breadth (Brown, 1984; Gaston *et al.*, 2000), with species that can exist under a wider range of environmental conditions sometimes exhibiting larger areas of occupancy (Borregaard & Rahbek, 2010). Accordingly, species with smaller areas of occupancy might be most affected by climate change, as they may be unable to disperse to new environments with more favorable conditions, or may have reduced ability to grow in a range of conditions. Although a limited sample, the species in this study did not follow these predictions: of the two most widespread species, one shrank and one grew, and the most restricted species, *B. scaber*, showed no change over time. This stasis may indicate either that *B. scaber* was not affected by climate change or that it lacks suffi-
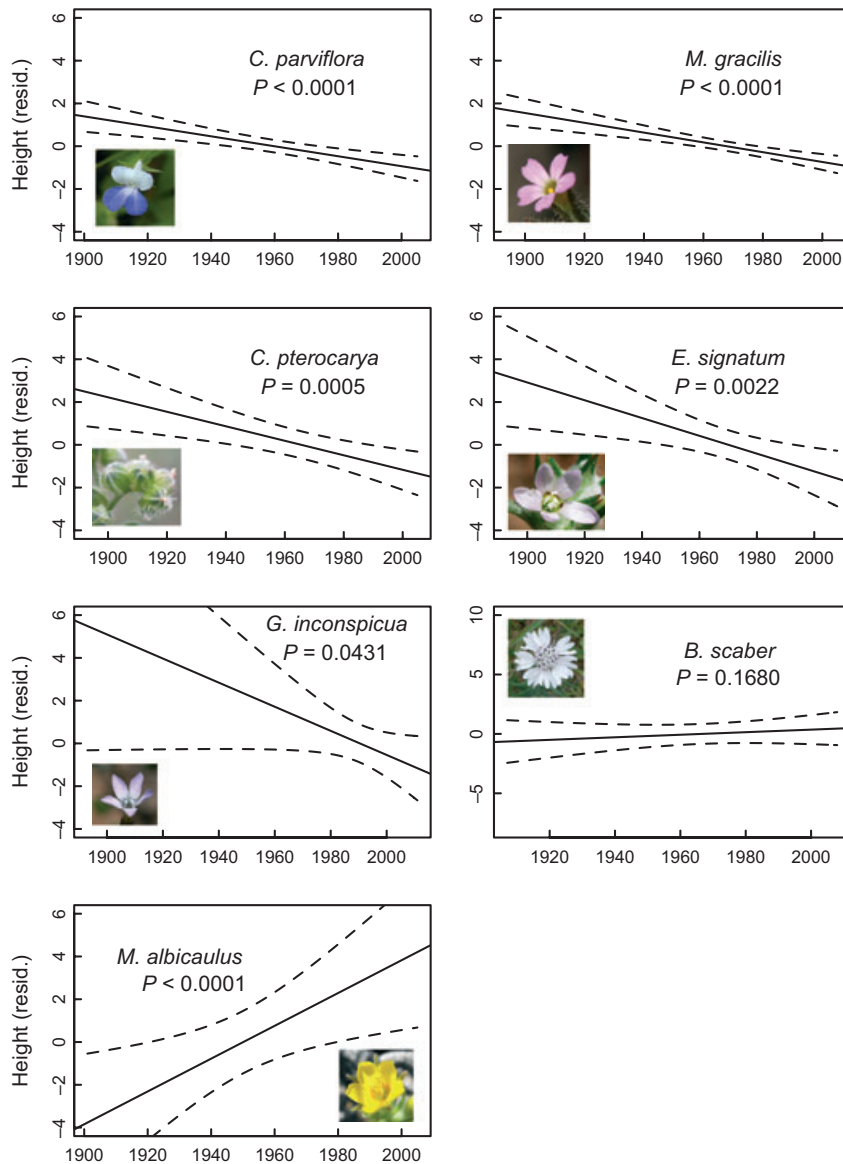
Fig. 3 Trends in residual plant height over time for seven annual forbs. Linear regressions (solid lines) and 95% CI (dashed lines) are shown. Residual heights are from a model fitted with elevation, latitude, longitude, plant collection date, and plant phenological stage. *P* values indicate significant year effect in the analysis depicted in Table 3; CI for the regression between year and residual heights shown in this figure do not overlap zero for all species except *Blepharipappus scaber* and *Gilia intermedia*. Slopes are as follows: *B. scaber*, 0.011; *Collinsia parviflora*, −0.023; *C. pterocarya*, −0.034; *Eriastrum. signatum*, −0.042; *G. intermedia*, −0.056; *Microsteris albicaulis*, 0.077; *M. gracilis*, −0.023, and represent the change in height (in cm) per year over the observation period.

cient plasticity to respond to changing conditions; observations of changes in population size over time could clarify the response of this species.

As neither climatic variables nor germination timing or distribution/abundance explained observed decreases in size, and in fact climate change would have been expected to lead to increases in plant size over time for many of these species, there is the possibility that other land-use factors of strong effect are responsible for synchronous changes in size among species that differ in ecological traits. The highly competitive invasive annual grass *B. tectorum*, by far the dominant invasive species in these systems, has increased in dominance in this region over the study period. Spreading rapidly after introduction in the 1890s, the plant expanded its range to approximately 400 000 km^2 after 1930 (Mack, 1981). *Bromus tectorum* has continued to increase in density, becoming the dominant plant over approximately 20 000 km^2 of the Great Basin

by the 1990s (Bradley & Mustard, 2005). Direct competitive effects of *B. tectorum* and effects of increased fire frequency associated with *B. tectorum* invasion could be reducing resources for native plants (Melgoza *et al.*, 1990; Whisenant, 1990; Blank *et al.*, 1994; Evans *et al.*, 2001). Cattle and sheep grazing also increased greatly during the observation period (Knapp, 1996; Young & Sparks, 2002), and grazing has been observed to decrease diversity in native annual plants in some low-productivity desert systems (e.g., Waser & Price, 1981; Osem *et al.*, 2002; Brooks *et al.*, 2006). Thus, the reductions in plant size observed in this experiment could result from multiple interacting factors, including climate change, extensive invasion, increased fire frequency, and grazing. Experiments that manipulated these factors could determine if land-use changes alone or interacting with climate changes could be responsible for observed decreases in size in this system.

Changes in plant height did not always result in parallel changes in flower numbers, doing so for only two species, one which decreased flower production and size (*C. parviflora*) and the other which increased in both size and flower production (*M. albicaulis*). There is typically a strong correlation between plant size and fecundity, especially for small annual plants, but this relationship can vary among sites (Aarssen & Taylor, 1992; Bazzaz *et al.*, 2000). The lack of change in flower number observed in four of six species that changed in size may indicate an ability to compensate for reductions in plant size with either increased allocation to reproduction in smaller plants, or with decreases in individual flower or seed size. In annuals, smaller plants typically have the same or smaller relative reproductive allocation as larger plants (Weiner *et al.*, 2009), so reduced individual flower or seed size may be more likely than increased reproductive allocation. Due to their small size, it would be difficult to measure these factors for these annual species on herbarium sheets, but this question may be amenable for larger herbarium specimens.

Museum collections and herbaria represent unique opportunities for research, housing specimens that can be used for molecular and chemical analyses, studies of range expansion or contraction, and responses to climate change (e.g., Brooks *et al.*, 1977; Savolainen *et al.*, 1995; Suarez & Tsutsui, 2004; Zangerl & Berenbaum, 2005; Guerin *et al.*, 2012). Certain limits are inherent in using such collections, and for this study, lack of information on plant density at the time of collection could be obscuring some ecological patterns. Specifically, an inverse relationship between size and density in intraspecific stands of plants is commonly observed

(Gorham, 1979), and there is the possibility that individual plants in particular years were small because population densities were high. Information on the effects of changing density on plant size are not available for these species, but if density strongly influenced plant size, some of the observed negative associations between size and climate might in fact reflect high population densities in those years, rather than unfavorable years. Increasing density is not, however, likely to be the cause for decreases in size over time, as invasion and land-use changes have led to wide-spread decreases, not increases, in native plant densities in this region (Knapp, 1996).

Reduced individual plant size may affect ecosystem productivity, directly influencing herbivores and pollinators, and by extension, result in fewer resources for predators. These particular annual forb species are of interest for their importance as food resources, as they are part of a guild of plants known to be important forage for sage-grouse, a bird of conservation concern in the Great Basin. Some of the species studied here, including *B. scaber, M. gracilis,* and *C. parviflora,* have been directly observed to compose part of sage grouse diets (Drut *et al.*, 1994; Gregg, 2006). If plant sizes and population densities of annual forbs are decreasing over time, this may negatively affect sage-grouse performance. There is some interest in enhancing annual forb populations to enhance the habitat value of sage-grouse habitat, and studies like this could identify species that can perform well under current conditions (e.g., *M. albicaulis*), which could be used in restoration. In addition, identifying climatic preferences of multiple annual species could help in designing a restoration mix that would include species likely to do well in many different kinds of climatic years, taking advantage of the portfolio effect (Tilman *et al.*, 1998) to ensure successful forb recruitment even under variable resource availability.

Determining whether observed changes are due to plastic responses to environmental change or to evolutionary shifts in these populations is challenging, given the lack of viable seeds from older collections and the lack of information on genes responsible for determining plant size for these species. An inferential method using information from the tissues that are available could possibly address this question in herbarium collections. In a study that documented decreases in body size of birds from museum collections, feather growth measurements were used to determine if birds were under increasing nutritional stress over time, with the rationale that reductions in size occurring independent of stress would be consistent with genetic change, rather than with a plastic response (Gardner *et al.*, 2009). It is possible that analyses of C : N or isotopic

signatures could be used to measure relative nutrient or drought stress over time in plants. The amount of plant material needed for these analyses would be impractical for annual plants, but such a technique could be used for larger specimens.

Finally, although most species in this study decreased in size over time, two species had contrary responses (either increasing in size or not changing), possibly indicating that they were not negatively affected by factors affecting other annual forbs. Species that increase in size or population density under climate change might represent those with generalist strategies and wide ecological niches, or species with a high degree of phenotypic plasticity (Sheridan & Bickford, 2011). Combined with field surveys of population size and plant density, herbarium records could be used to identify species that differ in their ability to cope with changing environments. Comparing traits of organisms that are decreasing in plant size or population density over time with those that are increasing may provide valuable information on the types of life history strategies most likely to be successful under current conditions, identifying priorities for conservation and the most likely candidates for successful restoration of native plant communities.

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