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GLOBAL CHANGE ECOLOGY – ORIGINAL RESEARCH

Does adaptation to historical climate shape plant responses to future rainfall patterns? A rainfall manipulation experiment with common ragweed

Amanda J. Gorton[1] · **Peter Tiffin**[2] · **David A. Moeller**[2]

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Abstract

Climate change is affecting both the volume and distribution of precipitation, which in turn is expected to affect the growth and reproduction of plant populations. The near ubiquity of local adaptation suggests that adaptive differentiation may have important consequences for how populations are affected by and respond to changing precipitation. Here, we manipulated rainfall in a common garden to examine how differentiation among populations of common ragweed, *Ambrosia artemisiifolia* (Asteraceae) affects responses to water availability expected under climate change. We collected seeds from 26 populations along gradients of historical rainfall and used event-based rainout shelters and watering additions to simulate drier summer conditions and more extreme rainfall events, respectively. *Ambrosia artemisiifolia* had higher fitness on average under reduced rainfall, suggesting it may spread and become more abundant in areas projected to become hotter and drier during the summer months. We also found strong evidence for phenotypic and fitness clines across both latitude and longitude, and that phenological responses and fitness effects of altered rainfall depended on seed source or historical climate. The effect of rainfall treatment on female fitness was highest in western and mid longitudes, but there was little effect on eastern populations. Across latitude, the effect of rainfall treatment on male fitness was highest in southern populations. These phenology and fitness clines suggest that adaptive differentiation across the species' range has the potential to shape future responses of *A. artemisiifolia* populations to climate change, particularly altered patterns of rainfall.

Keywords Local adaptation · Climate change · Local maladaptation · Range limits · Latitudinal gradient

Introduction

One key aspect of climate change for many organisms, including plants, is changing precipitation patterns (Trenberth et al. 2003; Weltzin et al. 2003; Wu et al. 2011). Over the next century the contiguous United States is projected to experience changes in both the overall volume and event severity of precipitation (IPCC 2013). In particular, total precipitation is projected to decline in all areas during the summer months while heavy precipitation events are projected to increase in frequency (IPCC 2013). This suggests that rain will likely fall in fewer, but more intense events during these key growing months.

Water availability is known to have consequences for plant development (Schwinning and Ehleringer 2001), physiology (Noy-Meir 1973; Dudley 1996), and species distributions (Engelbrecht et al. 2007). It follows that changes in precipitation will likely affect the growth and fecundity of individual plants and the dynamics of populations. In addition, precipitation changes may interact with rising temperatures, potentially imposing drier, drought-like conditions for plants. On the other hand, heavy precipitation events may cause episodic flooding or soil saturation, which could also impair plant–soil–water

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✉ Amanda J. Gorton
gorto019@umn.edu

[1] Graduate Program in Ecology, Evolution and Behavior, University of Minnesota, 1987 Upper Buford Circle, Saint Paul, MN 55108, USA

[2] Department of Plant and Microbial Biology, University of Minnesota, 1479 Gortner Avenue, Saint Paul, MN 55108, USA

relations and plant growth and development (Kramer 1951; Kozlowski 1992). By directly affecting the growth and fecundity of individual plants, this widespread and rapid change in precipitation has the potential to affect the geographic distribution of species as well as selection on populations (Franks et al. 2007). Responses of particular species or populations to altered water availability are, however, unclear.

Manipulative experiments have shown that increased precipitation often results in greater individual above-ground biomass and ecosystem productivity while decreased precipitation tends to suppress both (Wu et al. 2011; Didiano et al. 2016). However, the magnitude and direction of responses can vary among species (e.g., Campbell and Wendlandt 2013; Didiano et al. 2016). For example, Schneider et al. (2014) found that reduced watering led to a reduction in the biomass of the legume *Lupinus perennis*, but not in the C_3 grass *Agropyron repens*. Furthermore, there are mixed results as to whether geographic origin and climate influence the ecological and evolutionary responses of plants to altered precipitation patterns. A recent meta-analysis of experimental warming and precipitation found that plant biomass and net primary productivity did not vary among geographic locations that differed in mean annual temperature or mean annual precipitation (Wu et al. 2011). In contrast, a meta-analysis of the effect of local climatic factors on phenotypic selection in wild populations found that 50–70% of the variation in selection on traits was associated with variation in precipitation (Siepielski et al. 2017). However, phenotypic selection analyses cannot disentangle the effect of the environment on trait expression from that of genetics (Rausher 1992). Moreover, the environmental effects on trait expression can sometimes be opposite to patterns of genetic divergence (Conover and Schultz 1995; Eckhart et al. 2004; Gorton et al. 2018) thus phenotypic data, alone, may misrepresent expected adaptive responses to climate change.

The prevalence of local adaptation to climate (Turesson 1922; Clausen et al. 1940; Aitken et al. 2008; Leimu and Fischer 2008; Hereford 2009) indicates that adaptation has and will likely continue to play an important role in species persistence under future climates. Since the rate of contemporary climate change has occurred rapidly, population responses to selection could be constrained by limited standing genetic variation (Jump and Penuelas 2005; Hoffmann and Sgrò 2011). However, adaptation may be facilitated by gene flow, particularly if that gene flow occurs via the introduction of alleles from elsewhere in a species' range where historical climate better matches predicted future conditions (Davis and Shaw 2001; Sexton et al. 2011; Aitken and Whitlock 2012). Nonetheless, the extent to which potential gene flow might facilitate adaptation to future environments is dependent on the extent to which populations are adaptively differentiated.

Experimental manipulations of precipitation are required to disentangle evolutionary adaptation from phenotypic plasticity. Long-term observation of natural populations in response to climate can provide important insight into the ecological effects of ongoing precipitation changes on plant traits (e.g., Dunnett et al. 1998). However, observational data do not bear on adaptive differentiation because they inherently confound phenotypic plasticity with genetic differentiation. Furthermore, altered precipitation may be confounded with other covarying factors, such as temperature or CO_2 levels. Thus, experimental manipulations of precipitation in a common garden environment importantly complement observations of natural populations (Beier et al. 2012). While reciprocal transplant experiments are required to test for local adaptation, common garden experiments can allow patterns of genetic differentiation to be identified, and in turn, correlated with associated environmental differences at each collection site. Common garden experiments also offer greater control of confounding variables, allow multiple climate change scenarios to be studied simultaneously, and can more readily allow researchers to disentangle the contribution of the environment vs genetics to trait expression and their consequences for plant population responses to climate change.

Here, we manipulated rainfall onto plots in a common garden to ask how simulated changes in rainfall affect trait expression and lifetime fitness among populations of common ragweed, *Ambrosia artemisiifolia* (Asteraceae) and whether those responses varied relative to the historical climate experienced by those populations. Our experimental plants were grown in a common garden from seeds that we collected from source populations sampled along both latitudinal and longitudinal gradients as well as gradients of historical annual rainfall. We manipulated water availability through the use of event-based rainout shelters to reduce total rainfall and simulate drier summer conditions, and watering additions to increase total rainfall and simulate more extreme rainfall events. We collected data on ecologically important traits (flowering time, size, specific leaf area), and components of fitness (flower and fruit number). We address the following specific questions: (1) How will future rainfall patterns affect the growth, phenology, and fitness of *A. artemisiifolia*? and (2) What is the nature of phenotypic differentiation in response to historical climate variation along latitudinal and longitudinal gradients? and (3) To what extent does historical rainfall at collection origin predictive of the response to altered water availability, i.e., is the response dependent on the latitude and longitude or annual precipitation of each seed source?

Materials and methods

We conducted a rainfall manipulation experiment in Minnesota, in the northern portion of the species' range, using seeds sampled from populations across a large portion of the geographic range of *A. artemisiifolia* (Asteraceae). In the midwestern United States, the summer growing months are projected to become both hotter and drier on average, with a reduction of 10–30% in seasonal precipitation depending on the location (IPCC 2013; NOAA 2014). Furthermore, in the past 50 years, there has been a 37% increase in the amount of precipitation falling in heavy rainfall events (NOAA 2014, p. 9). Based on these historical trends and projections, we chose to reduce rainfall by 30% and increase rainfall by 30% for the reduction and addition treatments, respectively (see "Rainfall manipulation experiment").

Ambrosia artemisiifolia L. (Asteraceae) is a self-incompatible (Friedman and Barrett 2008), monoecious, and wind-pollinated (Jones 1936; Essl et al. 2015) annual plant native to North America and invasive on multiple continents (Bass et al. 2000; Chauvel et al. 2006). It is a ruderal plant that is often abundant in open, disturbed habitats such as river banks, roadsides, agricultural fields, and urban areas. *Ambrosia artemisiifolia* is a summer annual that typically germinates in late spring in Minnesota (May–June) and flowers in late summer. It is sensitive to freezing and can be killed by late spring and early autumn frosts; the latter terminates the growing season.

The transition to reproduction is cued by photoperiod and is initiated when the length of day shortens sufficiently after the summer solstice. Staminate capitula (i.e., male flowering heads) are found in spike-like racemes, hereafter referred to as 'male flowers', which produce the pollen that is one of the primary causes of summer and fall allergic rhinitis (Lewis et al. 1983; Frenz 2001). Pistillate capitula (i.e., female flowering heads) are found in axillary clusters below the male flowers; each individual flower develops into an achene (a small, single seeded fruit) which readily falls off the plant once ripe. These groups of achenes are hereafter referred to as 'fruits'.

Seed collections

During Oct 2015–Jan 2016, we collected seeds from 26 populations of *A. artemisiifolia* across a region spanning 15° of latitude (~ 1700 km) and 7° of longitude (~ 550 km). These populations have experienced a wide range of historical combinations of temperature and precipitation (Figure S1, Table S1). The sampling area includes both a north–south and an east–west precipitation gradient that ranges from a low of 609 mm per year in eastern South Dakota to a high of 1595 mm per year in southern Louisiana (precipitation data from WorldClim 2.0). Sampling sites were on average 290 km apart along each latitudinal transect, and when two populations were sampled at a given latitude, we collected separate populations in both urban and rural environments because the phenotypes of urban and rural populations of *A. artemisiifolia* differ from those of rural populations (Gorton et al. 2018). At each sampling site, we collected seeds from 16–25 maternal plants, each separated from the rest by at least 3 m.

Rainfall manipulation experiment

In May 2016, we planted a single common garden on the University of Minnesota campus in Minneapolis, Minnesota, in a previously abandoned field (44.9763, − 93.21948) that was densely occupied by weeds. Prior to planting seeds, we sprayed the area with glyphosate and tilled with a tractor to remove existing vegetation, creating an environment similar to the disturbed, low-competition habitats where ragweed most often occurs.

We established 30 rainfall treatment plots (10 reduction, 10 addition, 10 control) in a 9 column × 3–4 row grid with 1 m spacing on all sides around each plot (Figure S2). The planting spacing within each plot was designed to mimic natural growing densities of *A. artemisiifolia* (Foster et al. 1980; MacDonald and Kotanen 2010). The plots alternated across the grid to ensure the rainfall treatments were distributed evenly across the study area. The 3–4 plots in each column constituted a 'block' (Figure S2). We chose blocks in this way because the columns occurred perpendicular to a gradual slope that had the potential to influence rainfall runoff and soil moisture. Each plot measured 2 m^2 and included a 40 cm border from the edge of the experimental plants to the edge of the plot. Each plot contained seeds from one to two different families from each of the 26 populations, for a total of 45 seeds per plot, planted in a completely randomized design. A total of 16–25 families per population were included in the experiment (total number of families = 367) (Table S1).

Ambrosia artemisiifolia has strong dormancy, with viable seeds remaining in the seed bank for up to 40 years (Toole and Brown 1946). To minimize the potential to confuse experimental plants with plants that grew from seeds in the seed bank, we used the ProPlugger (ProPlugger, NC) to remove a soil plug (5 cm × 5.5 cm) at each planting spot. The holes were then filled with B2 germination mix (Berger, Quebec). The seeds were stratified in moist silica sand to break dormancy, and kept in the dark at 4 °C for 10 weeks (Willemsen 1975). At each planting spot, we planted 2–4 stratified seeds from a given maternal family directly into the ground from 31 May to 3 June 2016, and watered the seeds once immediately after planting (total number of seeds planted = 4515). Plants in the reduction and control plots were not watered again for the duration of the experiment. Two weeks after planting, plants were thinned to a single seedling per planting spot. Throughout the growing season, all plots were regularly weeded to minimize interspecific competition.

We used event-based rainout shelters for our reduction treatments. These types of shelters are removable and are deployed to exclude specific rainfall events rather than remain in place for the duration of the growing season (e.g., Eisenhauer et al. 2012; Reich et al. 2014). Consequently, they minimize microhabitat effects on the underlying vegetation, including shading, passive warming, and altered humidity and wind (Beier et al. 2012). We designed and constructed the rainout shelters using PVC pipes and clear, overwintering greenhouse plastic (Figure S3). Beneath the lowest point of the roof of each reduction plot, we placed a rain barrel to collect excluded rainfall. We also placed a rain gauge in the center of each reduction plot to determine if the rainout shelters failed during an excluded rainfall event.

We conducted the rainfall manipulation treatments by attaching the roofs of the rainout shelters for 11 rainfall events from 30 June 2016 until 20 September 2016. We removed the rainout shelter roofs the day after a rainfall event, and recorded the total rainfall in uncovered rain gauges. We calculated the total reduction in rainfall from June to September as the ratio of the summed recorded rainfall in the rain gauges on the days we deployed the rainout shelters to the total rainfall for the season, obtained as the sum of the amounts in the rainfall gauges over the whole season. Based on these data, we excluded approximately 30% of total rainfall from the exclusion plots.

For the addition plots, we added supplementary water the day after an excluded rainfall event ($n = 11$) to increase rainfall by 30%. We multiplied the rainfall depth recorded in the uncovered rain gauges by the area occupied by plants in each addition plot (1.69 m^2) to calculate the volume of water to be added to each addition plot. We used water from the rain barrels, when available, and applied it to the addition plots using watering cans to evenly distribute the water. Early in the season when rain barrels were empty, we used tap water for the addition treatments.

Phenotypic and environmental data collection

Each week we recorded whether each plant was in a vegetative or reproductive phase and whether they had produced their first male and female flower. The transition to reproduction was scored as the date of the first appearance of a reproductive bud at the apical meristem. The first male flower was scored as the date on which the first anther opened and shed pollen, i.e., the first open male flower, and the first female flower was scored as the date at which stigmas first appeared. We also measured plant height at 8 and 19 weeks after planting.

We estimated specific leaf area (SLA), the ratio of leaf area/leaf dry mass (cm^3/g) as a proxy for water use efficiency (Reich et al. 1991; Poorter and Bongers 2006). We estimated SLA using the first fully expanded leaf from each plant 8 weeks after planting, approximately 4 weeks after the start of the rainfall treatments. We stored all leaves at 4 °C in individual ziplock bags with a moist paper towel to prevent wilting, and scanned them within 3 days of harvest with a leaf area meter (LI-Cor LI-3000A Portable Area Meter and LI-3050A Transparent Belt Conveyor), followed by drying at 55 °C for 7 days. Once the leaves were completely dry, we weighed them to obtain dry mass.

We estimated fitness at the end of the growing season between 24 September and 11 October, which was after individuals stopped growing and when plants begin to senesce. Based on data from 1981 to 2010, there is a 50% chance of a frost occurring by 5 October (0 °C, U.S. Climate Normals, NOAA). It was not possible to quantify male and female fitness across whole plants due to their size and the narrow time window over which data collection needed to occur. Instead, we systematically subsampled branches across each plant to account for potential variation in allocation to male versus female reproduction across plant development (ca. 20–50 total branches/plant). On each plant, we counted the number of flowers and fruits on every fourth branch, starting with the lowest and largest branch, and moving up towards the apical meristem. We multiplied this number by four to get a whole-plant estimate of male and female fitness.

We collected data on soil moisture (volumetric water content, VWC) every hour from the time seeds were planted to the time of harvesting, using ECH_20-E5 Decagon soil moisture sensors and Em50 ECH_20 data loggers. We buried soil moisture probes in the center of 10 treatment plots and inserted them horizontally at a depth of 30 cm (4 reduction plots, 4 addition plots, and 2 control plots). Due to probe malfunctioning (negative VWC values and/or incorrect dates), we were unable to obtain data from the beginning of the rainfall manipulation treatments; usable data began around 29 July 2016, approximately 1 month after the start of the rainfall treatments. Data from the soil moisture probes indicated the reduction plots had drier soil than the control and addition plots (Figure S4), indicating the efficacy of our treatments in altering water availability.

We extracted historical precipitation data (1970–2000) based on the latitude and longitude of each collection site from WorldClim 2.0 (Fick and Hijmans 2017). We downloaded the BIOCLIM precipitation variables (BIO12–BIO19) for each location at a spatial resolution of 5 m.

Statistical analysis

To determine how phenology (date of transition to reproductive phase, date of first open male flower, date of first open female flower), height (at 8 and 19 weeks after planting) and SLA responded to the rainfall treatments, we fit linear models (LMs, *lme4* package, Bates et al. 2015) with rainfall treatment as the explanatory variable of interest. In these models we also included block (column in which each plot occurred) and edge (whether the individual plant was on the edge or center of the treatment plot) as categorical variables to account for effects of microenvironmental variation across the field site (Figure S2). We ran separate models with each of the three phenology traits (date of transition to reproductive phase, date of first male flower, date of first female flower), each of the two height measurements (height at 8 weeks, height at 19 weeks), and SLA as the dependent variables. We tested for differences among rainfall treatments using Tukey's tests implemented in the *multcomp* package (Hothorn et al. 2008). In addition, since we conducted the same analysis on six phenotypic traits, we adjusted the alpha level required to infer significance for each test using a sequential Holm–Bonferroni correction (Holm 1979) using *p.adjust*() in base R.

Many climate variables, including annual precipitation, annual temperature, and growing season length are highly correlated with one another as well as with latitude or longitude. Consequently, to examine the effect of seed source on the response to rainfall treatment, we conducted two sets of analyses with different environmental predictors. The first used latitude and longitude as predictors, considering them proxies for historical climate and other geographically variable environmental factors. Due to the low range of longitudes included across the sampled populations, we binned longitude into three categories for all analyses: (1) longitudes greater than 94° ('western'), (2) longitudes between 92° and 94° ('central), and 3, longitudes less than 92° ('eastern'). In the second set of analyses, for each collection site we used the value for the first principal component (PC1) of the seven BIOCLIM precipitation variables as a predictor (PC1 accounted for 85% of the variation, Table S2, S3). PCs were obtained using *princomp*() in base R. To determine whether phenology, height and SLA varied with latitude and longitude of seed source and rainfall treatment, we fit LMs with block (column in which each plot occurred), edge (whether plant was located on the edge or the middle of plot), latitude and longitude of origin of each population, rainfall treatment, latitude × longitude, latitude × treatment, and longitude × treatment as predictors. We ran similar models with the precipitation PC1, instead of latitude and longitude, as a predictor. We also tested for non-linearity in the relationship between each trait and latitude by including latitude^2. In cases where the quadratic term was significant, we fit splines using *smooth.spline*() to examine the shape of the relationship. For each of the phenology and size traits, latitude^2 explained a small proportion of the variance, and was statistically significant only for height at 8 weeks (Table S4). There was no evidence of any major curvature or a plateau in our data (Figure S5); therefore, we have presented only the linear analyses in the results below.

In both sets of analyses, as before, we tested for differences among rainfall treatments using Tukey's tests and controlled for multiple testing using a sequential Holm–Bonferroni correction (Holm 1979). For all LM analyses, we determined the significance of the predictors and interactions using *F* tests and estimated percent variance explained using Type II sums of squares with the car package (Fox and Weisberg 2011). Least-square means were extracted for plots from each model using the emmeans package (Lenth 2016).

To determine how lifetime fitness was affected by rainfall treatment and whether it varied among seed sources, we used fixed effects models in '*aster*' (*aster* package, Geyer et al. 2007; Shaw et al. 2008). *Aster* explicitly models the dependence of fitness components expressed later in development (e.g., fecundity) on those expressed earlier (e.g., survival) and allows for different statistical distributions for each fitness component. For each individual, we used the following graphical model to estimate lifetime female fitness (number of fruits):

$$1 \rightarrow \underset{(0,1;\ \text{Bernouilli})}{\text{Survival to 8 weeks}} \rightarrow \underset{(0,1;\ \text{Bernouilli})}{\text{Any fruit or flowers (Y/N)}} \rightarrow \underset{(\text{Zero truncated Poisson})}{\text{Number of fruit}}$$

The same model was used for male fitness, except that the number of male flowers replaced number of fruits. In addition to the response variable of lifetime fitness, we included the same predictors as above (block, edge, latitude, longitude, latitude × longitude, latitude × treatment, longitude × treatment). We ran similar models with the precipitation PC1, substituting PC1 for latitude and longitude. As in our LMs, we also tested for non-linearity between fitness and latitude by including latitude^2, and fit splines using *smooth.spline*() to examine the shape of the relationship. As there was evidence for a significant effect of latitude^2 on both male and female fitness, we also tested whether this relationship changed depending on the rainfall treatment by including latitude^2 × treatment. We determined the significance of all fixed effects and interactions by sequentially comparing nested models with and without the term of interest using likelihood ratio tests. For significant interactions, we predicted male and female lifetime fitness separately for each combination. Hereafter, predictions of lifetime fitness from the aster models are referred to as 'fitness'.

To better understand how individual components of fitness responded to treatments and jointly contributed to lifetime fitness, we ran separate GLMs for each of the three fitness components: survival to 8 weeks, probability of fruiting (female) or flowering (male), and number of fruits or flowers. We used a binomial error distribution and logit link function for survival to 8 weeks and probability of flowering/fruiting, and a Poisson error distribution and log link function for number of fruits and number of flowers. Unlike the analyses we ran in *aster*, these analyses are conditional such that individuals are only included in the analysis if they successfully reached that life history stage (e.g., only plants that survived to 8 weeks are included in the analyses for probability of fruits). In addition to treatment, these models also included edge and block as predictors. We determined the significance of each predictor using F tests and estimated percent variance explained using Type II sums of squares with the *car* package (Fox and Weisberg 2011). Least-square means were extracted for each fitness component using the emmeans package (Lenth 2016). All analyses were conducted in R, 3.2.2 (R Core Team 2015).

Results

Effect of rainfall treatment on traits and fitness

We detected no overall effect of rainfall treatment on either the date at which plants transitioned to reproduction or flowered ($p > 0.5$ for all phenology traits, Table S5, Fig. 1a). Plants in the reduction treatment were on average 4 cm shorter than those in the other treatment plots after 8 weeks of growth ($p < 0.001$; Table S5, Fig. 1b), but this effect disappeared by the end of the growing season ($p > 0.9$; height at 19 weeks, Table S5). Rainfall treatment also had an effect on specific leaf area (SLA) ($p < 0.05$, SLA, Table S5, Fig. 1c); plants in the addition plots had significantly higher SLA (thinner leaves) than those in the control plots (Tukey contrast: $p = 0.003$). Plants in the addition plots also had higher SLA than those in the reduction plot, but this difference was not statistically significant (Tukey contrasts: $p = 0.11$). Fitness differed strongly among treatments: plants in the reduction plots had 31–38% higher male and 16–25% higher female fitness than plants in the control and addition plots, respectively ($p = 0.04$ for female fitness, $p < 0.0001$ for male fitness, Table S6, Fig. 2a, b). Plants in the control plots also had 4% higher male and 8% higher female fitness than those in the addition plots.

In our conditional analysis of each life history component in the *aster* model, we found a significant effect of treatment on survivorship at 8 weeks ($p_{\text{Wald } \chi^2=9.03, df=2} = 0.01$), number of fruit ($p_{\text{Wald } \chi^2=1592.3, df=2} < 0.0001$), and number of male flowers ($p_{\text{Wald } \chi^2=2280.3, df=2} < 0.0001$). Mean survivorship at 8 weeks in the addition, control and reduction

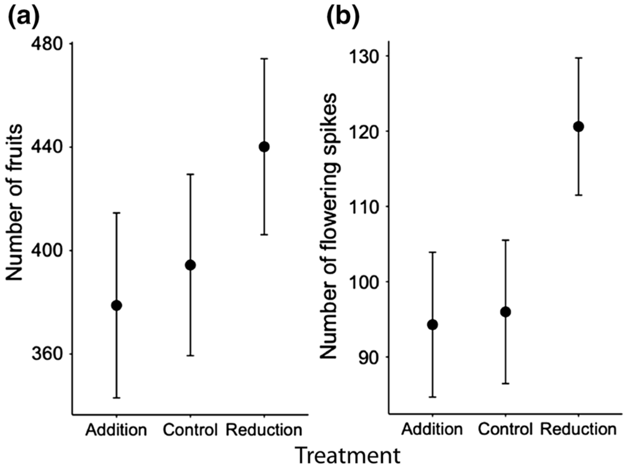

Fig. 2 Effects of rainfall treatment on **a** mean number of fruits (female fitness), and **b** mean number of flowering spikes (male fitness). Predicted means were extracted from *aster* models and are presented with standard error bars

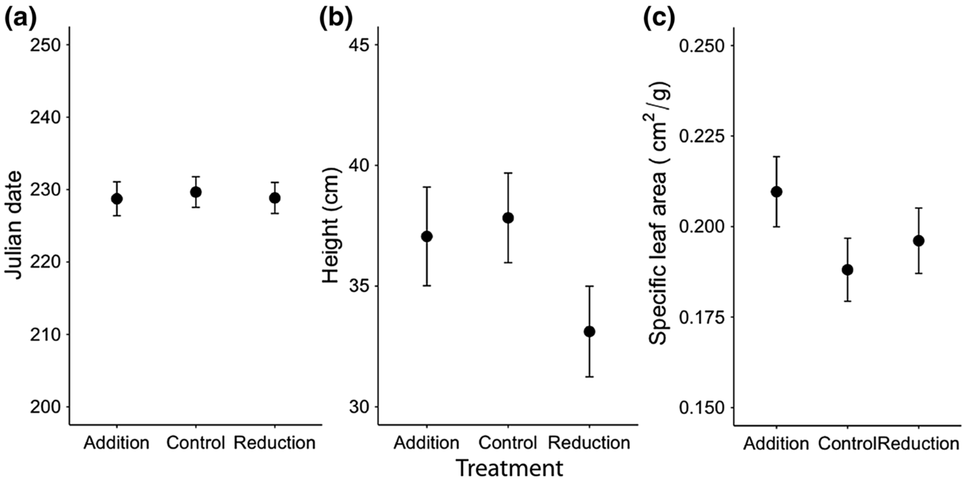

Fig. 1 Effects of rainfall treatment on **a** mean Julian date of transition of reproduction, **b** mean height at 8 weeks, and **c** mean specific leaf area. Least-square means were extracted from linear models and are presented with standard error bars

treatment was 57.3%, 68.5%, and 64.1%, respectively. The mean number of fruits in the addition, control and reduction treatment was 740, 665, and 761 fruits, respectively, and the mean number of male flowers in the addition, control and reduction treatment was 192, 161, and 224, respectively. We did not detect an overall effect of treatment on either probability of fruiting ($p_{\text{Wald } \chi^2=1.5, df=2} = 0.47$, addition = 90.5%, control = 90.3%, reduction = 92.8%) or flowering ($p_{\text{Wald } \chi^2=0.41, df=2} = 0.81$, addition = 84.2%, control = 86.1%, reduction = 84.3%).

Interactive effects of rainfall treatment and geographic origin on traits

Flowering time varied among populations along both latitudinal and longitudinal clines. Averaged across treatments, populations from northern latitudes and eastern longitudes initiated reproduction and flowered earlier than populations from southern latitudes and western longitudes (latitude: $p < 0.0001$; longitude: $p < 0.05$ for all phenology traits, Table S7). The relationships between transition of reproduction, time to first open male flower and geographic origin were also affected by rainfall treatment (latitude × treatment: $p = 0.005$ for transition of reproduction, $p = 0.02$ for time to first open male flower, Table S7), although the p value for time to first open male flower was > 0.05 after controlling for multiple testing. In general, plant populations from more southern latitudes initiated reproduction and flowered earlier in response to the rainfall reduction, whereas those from northern latitudes flowered at similar times across all three treatments (Figure S6).

Size at both 8 and 19 weeks also displayed latitudinal clines ($p < 0.01$, Table S7). Populations from southern latitudes tended to be taller, and this effect was more prominent at the end of the growing season (Figure S7). SLA was lower in western than in eastern populations ($p = 0.006$; Table S7, Figure S8), but there was no significant difference among the longitude categories (Tukey's test: $p > 0.05$ for all comparisons) or with latitude ($p = 0.07$; Table S7).

Interactive effects of rainfall treatment and geographic origin on fitness

In general, plants in the reduction plots had the highest female fitness, but the magnitude of difference among rainfall treatments depended on the source longitude (treatment × longitude: $p = 0.03$, Table S8, Fig. 3). Populations from eastern longitudes had similar female fitness in all rainfall treatments, while those from central and western longitudes had the highest female fitness in the reduction plots and the lowest fitness in the addition plots. Female fitness was also related to the latitude of the source population and this relationship was non-linear (latitude^2: $p < 0.0001$, Table S8) that was largely driven by the lower fitness of southern populations (Figure S9a) and was not affected by treatment (latitude^2 × treatment: $p = 0.33$, deviance = 2.24).

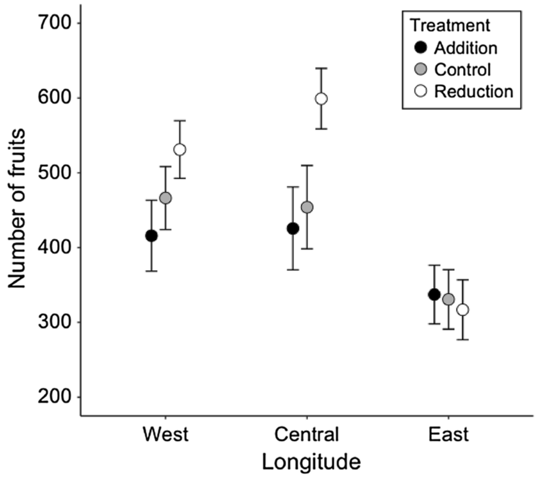

Fig. 3 Effects of rainfall treatment and longitude on mean number of fruits (female fitness). Predicted means were extracted from *aster* models and are presented with standard error bars

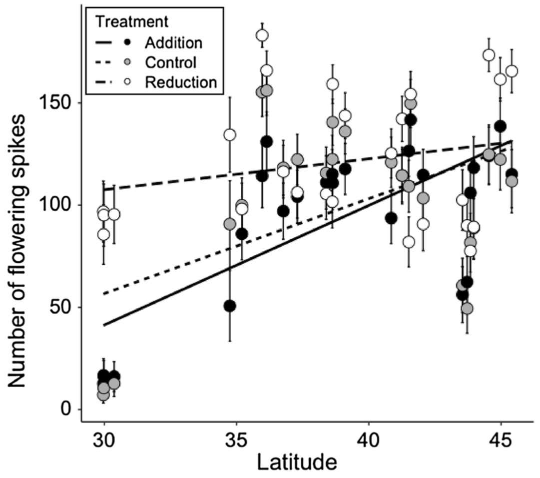

Fig. 4 Effects of rainfall treatment and latitude on mean number of flowering spikes (male fitness). Predicted means were extracted from *aster* models and are presented with standard error bars. Linear regression lines are shown for male fitness vs latitude for each rainfall treatment

Similar to female fitness, plants in the reduction plots had the highest male fitness, with rainfall treatments having the greatest effect on populations from southern latitudes (treatment × latitude: $p = 0.0004$, Table S8, Fig. 4). Male fitness of populations from southern latitudes (< 35°), was approximately 5–9 times higher in the reduction plots compared to those in the addition or control plots. There was evidence for non-linearity in the relationship between male fitness and latitude (latitude^2: $p < 0.0001$, Table S8) that was again likely driven by the lower fitness of southern populations (Figure S9b). Unlike female fitness, however, the nonlinear relationship between male fitness and latitude varied with treatment (latitude^2 × treatment: $p = 0.001$, Table S8), whereby individuals from the most southern populations had much higher fitness in the reduction plots than in addition and control plots (Figure S9b).

Both female and male fitness varied with both the latitude and longitude of source populations, and these effects were not uniform across either latitude or longitude (latitude × longitude: $p < 0.0001$, Table S8, Figure S10). Populations from higher latitudes and western longitudes had lowest female fitness whereas populations from eastern longitudes and mid latitudes had the highest female fitness. Populations from central longitudes had similar female fitness across all latitude of origin. The patterns were similar for male fitness, except that populations from higher latitudes and central longitudes had higher male fitness than those from eastern and western longitudes.

Interaction effects of rainfall treatment and source climate on traits and fitness

The effects of the precipitation variables, as summarized by PC1, were similar to the effects estimated for latitude and longitude. On average across treatments, populations from locales with historically higher precipitation flowered later (PC1: $p < 0.0001$, for all phenology traits, Table S9). The relationships between transition of reproduction, time to first open male flower and source climate were also affected by rainfall treatment. (PC1 × treatment: $p < 0.03$ for transition of reproduction and first open male flower, Table S9, Figure S10), although the probability of this occurring by chance was > 0.05 after controlling for multiple tests. Populations from wetter climates tended to transition to reproduction and flower earlier in response to the rainfall reduction than populations from drier climates, which transitioned to reproduction later under reduced rainfall. Populations from wetter climates also tended to be taller at the end of season (PC1: $p < 0.0001$ for height at 19 weeks, Table S9). SLA was not associated with source climate (PC1: $p = 0.65$; Table S9).

On average, populations from wetter climates had lower male and female fitness relative to those from drier climates (PC1: $p < 0.0001$, Table S10, Fig. 5a, b). There was a significant interaction between source climate and rainfall treatment for male fitness (PC1 × treatment: $p = 0.02$, Table S10) but not female fitness (PC1 × treatment: $p = 0.44$, Table S10). However, there was no major difference in slope among treatments for male fitness (Fig. 5b).

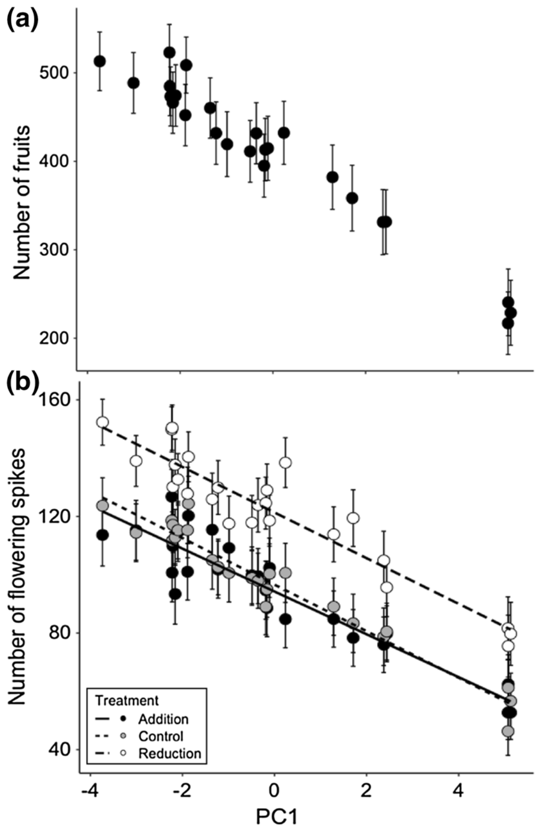

Fig. 5 Effects of PC1 of BIOCLIM precipitation values on **a** mean number of fruits (female fitness), and **b** mean number of flowering spikes (male fitness). Linear regression lines are shown in **b** for male fitness vs PC1 for each rainfall treatment. Predicted means were extracted from *aster* models and are presented with standard error bars

Discussion

Differentiation across a species' range might have important consequences for how populations are affected by ongoing climate change and their potential for range shifts. One might expect that populations that have experienced histories similar to future climates will be less affected. Gene flow among populations might also mitigate effects of climate change on fitness by introducing adaptive genotypes or alleles from populations that have adapted to similar climates present elsewhere in the range. The effects of local adaptation have begun to be integrated into species distribution models (Hällfors et al. 2016; Peterson et al. 2018) and empirical work (Aitken et al. 2008; Wadgymar et al. 2018) that predict responses to climate change. However, we are not aware of any empirical experiments that have incorporated local adaptation to historical precipitation to predict plant responses to future rainfall patterns.

The results from our manipulative experiments provide some support for the hypothesis that adaptive differentiation may shape population responses to future rainfall environments. We found that ragweed populations generally had higher fitness under reduced rainfall, and we found strong evidence for phenotypic clines across both latitude and longitude. Although the overall effects of rainfall treatment and seed sources were much stronger than the interaction between the two, the phenological responses to and fitness effects of altered rainfall varied among populations in relation to their historical climate. Populations from western longitudes with historically drier climates tended to have higher fitness in the reduction treatment and also had the largest SLA, suggesting adaptive differentiation in response to precipitation. However, populations from southern latitudes, which have historically wetter climates, also had highest male fitness under reduced rainfall. While these results appear to be in conflict, they are most likely due to the interaction between latitude and longitude: western longitudes are consistently dry across latitude, whereas eastern longitudes are only dry at northern latitudes. In addition, there are other environmental variables (e.g., temperature and photoperiod) that are changing across latitude and longitude which likely influence plant fitness. Nonetheless, the correlations between historical rainfall and performance under manipulated rainfall suggest that adaptive differentiation may determine the response of *A. artemisiifolia* to the direct effects of altered rainfall under climate change. Given this geographic variation, it follows that gene flow among populations has the potential to introduce alleles that confer higher performance under projected drier conditions during summer months.

Phenotypic responses to rainfall manipulation

Manipulative experiments have found that increased rainfall generally increases plant growth and reproduction, while reduced rainfall limits it (Wu et al. 2011; Didiano et al. 2016). We found the opposite pattern: *A. artemisiifolia* had the highest fitness in the reduction treatment, and lowest fitness in the addition treatment. This effect was not caused by greater interspecific competition in the increased rainfall treatment as we prevented differences in surrounding plant growth across treatments by weeding. Plants in the reduced rainfall treatment also had thicker leaves, suggesting reduced water availability may lead to lower SLA values.

Overall, these results suggest that populations in the portion of the species' range that currently experience the highest rainfall (mid-central southern United States), may increase in size in response to the reduced rainfall that is predicted over the next 100 years (IPCC 2013). This portion of the species' range (including AR, OK, KS, TX and LA) lies at the southern extent of the range where populations are considerably less common than in other parts of the range of *A. artemisiifolia* (Kartesz 2015). At the northern portion of its range, summer rainfall also is projected to decrease under a high emissions scenario although much less dramatically than in the south (IPCC 2013). Therefore, *A. artemisiifolia* may expand its range in the northern portion as well. Unlike the responses of many species to climate change, these results suggest *A. artemisiifolia* may expand its range and become more abundant, in particular at the southern portion of its range due to changing precipitation patterns. Nonetheless, our conclusions should be viewed with some caution given that a portion of the summer in which we conducted the experiment was particularly wet (the sixth wettest August on record for Minneapolis). Indeed, the high volume of ambient rainfall may provide one explanation for the reduced female fitness under the addition treatment, at least for populations from central and western longitudes which may be better adapted to drier environments than the populations sampled from eastern longitudes. As we discuss below, experiments over multiple years are needed in order capture the effects of extreme events on plant growth and reproduction.

Latitudinal and longitudinal clines of phenotypic differentiation

In our common garden, we found strong evidence for among-population trait divergence across latitude and longitude. Flowering time and height varied across both latitude and longitude of sources and these clines were associated with fitness: northern and western populations flowered earlier, were shorter, and had higher fitness than southern and eastern populations. There also was a longitudinal cline in SLA, whereby western populations had thicker leaves than eastern populations. Given that flowering time, size and SLA are often ecologically important traits in herbaceous plants, these clines are suggestive of local adaptation to environmental variation across the native range. However, neither latitude nor longitude impose selection. Rather these are proxies that serve to capture geographic variation in temperature, water availability and growing season length, and other environmental factors. Although it is likely a combination of environmental variables has caused these phenotypic clines, our experiment cannot determine which environmental factors are the causative drivers of selection, assuming that the differences are in fact adaptive.

The phenotypic divergence we found may have important consequences for range shifts under climate change. Our results indicate that there is widespread phenotypic differentiation across the species' range, suggesting that ragweed may readily adapt to new climatic conditions either in situ or at the expanding range edge. Furthermore, gene flow could facilitate adaptation, especially in plants with high dispersal capacity such as those with wind-dispersed pollen or seeds. Indeed *A. artemisiifolia* has historically experienced large and rapid changes in its distribution corresponding with Pleistocene climate change and subsequent human activity (Martin et al. 2014). Our results and these historical distribution patterns suggest that *A. artemisiifolia*, and perhaps other species with widespread distributions and high dispersal capacity, may have high range-shifting potential due to the ability to migrate, to adapt to new environments, and gene flow.

Latitudinal clines in ecologically important traits are commonly found in widely distributed, temperate plant species (e.g., *Arabidopsis*: Agren & Schemske 2012; *Poplar*: Keller et al. 2011, and have been previously documented in *A. artemisiifolia* in North America (Hodgins and Rieseberg 2011), Europe (Leiblein-Wild and Tackenberg 2014) and China (Li et al. 2014). These clines likely reflect adaptation to growing season length, summer temperatures and water availability. Longitudinal clines like those we found are less often reported. Given that daylength does not change across longitude, these clines in ecologically important traits (e.g., flowering time, SLA, etc.) may offer an opportunity to disentangle which environmental variables underlie adaptive differentiation (Samis et al. 2008, 2012). Furthermore, the interaction between latitude and longitude for fitness indicates that migration due to climate change might not be as simple as plant distributions shifting northwards as the climate warms. Instead, the east–west migration of populations or alleles across longitude may be equally important to the potential for range shifts and adaptation of plant populations in response to changing environmental conditions.

The effect of adaptive differentiation on plant responses to climate change

If local adaptation strongly affects plant phenological responses and fitness under climate change, we might expect populations to vary in their response to the rainfall treatments based on their geographic origin, and as a consequence, vary in their ability to cope with changing precipitation patterns in the future. However, the consequences of intraspecific variation for fitness and phenology under simulated rainfall conditions are still largely unknown (Liancourt et al. 2013). Those which have incorporated intraspecific variation into experimental manipulations of rainfall have either focused on functional traits in long-lived species (e.g., *Quercus*: Cavender-Bares and Ramírez-Valiente 2017; Ramírez-Valiente and Cavender-Bares 2017; Ramírez-Valiente et al. 2018; *Fagus*: Baudis et al. 2014) or examined biomass in response to both temperature and precipitation (Beierkuhnlein et al. 2011). In contrast, we are not aware of studies of lifetime fitness in response to rainfall manipulation.

In our experiment, there were some intriguing patterns that suggest adaptive differentiation may be important to predicting species' responses to future rainfall conditions. Populations from southern climates flowered earlier under reduced rainfall while populations from northern climates flowered later. Although we cannot determine what processes underly these patterns nor can we unequivocally state they are adaptive, one hypothesis is that populations from different climates have alternate plastic responses to drier conditions. Populations from southern latitudes or historically wetter environments may respond to dry conditions by flowering rapidly, while those from northern latitudes may tolerate dry conditions and flower later. We cannot exclude the potential for maternal environmental effects to have contributed to the patterns we found, as we used field collected seeds. However, maternal environmental effects are more likely to influence an individual's phenotype during earlier life stages (reviewed in Roach and Wulff 1987), and have not been previously found in *A. artemisiifolia* (Hodgins and Rieseberg 2011). We also found that populations from western climates had higher SLA across all treatments and higher female fitness in the reduction treatment, while populations from eastern longitudes had lower SLA across all treatments and similar fitness across treatments. Given that western populations experience lower annual precipitation, these results suggest potential adaptive differentiation in response to water availability and indicate that local adaptation may contribute to variation in the ability of different populations to respond to changing rainfall patterns. To develop a more complete understanding of how adaptive variation among populations might affect responses to climate change, it would be beneficial to extend the experiment we conducted over multiple years. This would assist in determining the extent to which population differences are affected by the absolute amount of rainfall as well as interacting factors such as temperature (Wu et al. 2011; Beier et al. 2012). Nevertheless, our results provide new information on how rainfall regimes affect lifetime fitness of genotypes from across a species' range and thereby influence the potential for range shifts.

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Author contribution statement AJG, PT, and DAM conceived and designed the experiment. AJG conducted all seed collections and conducted the field experiment. AJG conducted all data analyses, with advice and assistance from DAM and PT. AJG, PT, and DAM wrote the manuscript.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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