Role of climate and competitors in limiting fitness across range edges of an annual plant

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Abstract. It is often assumed that the geographic distributions of species match their climatic tolerances, but this assumption is not frequently tested. Moreover, few studies examine the relative importance of abiotic and biotic factors for limiting species ranges. We combined multiple approaches to assess the extent to which fitness of a widespread native annual legume, *Chamaecrista fasciculata*, decreases at and beyond its northern and western range edges, and how this is influenced by the presence of neighbors. First, we examined plant fitness and the effect of neighbors in natural populations at different geographic range locations for three years. Fitness decreased toward the northern range edge, but not the western edge. Neighbor removal had a consistently positive effect on seedpod production across all years and sites. Second, we established experimental populations at sites within the range, and at and beyond the northern and western range edges. We tracked individual fitness and recorded seedling recruitment in the following year (a complete generation) to estimate population growth rate. Individual fitness and population growth declined to near zero beyond both range edges, indicating that *C. fasciculata* with its present genetic composition will not establish in these regions, given conditions currently. We also carried out a neighbor removal treatment. Consistent with the natural populations, neighbors reduced seedpod production of reproductive adults. However, neighbors also increased early-season survival, and this positive effect early in life history resulted in a net positive effect of neighbors on lifetime fitness at most range locations. Our data show that the population growth rate of *C. fasciculata* includes values above replacement, and populations are well adapted to conditions up to the edge of the range, whereas the severely compromised fitness at sites beyond the edge precludes immediate establishment of populations and thereby impedes adaptation to these conditions.

Key words: aster models; Chamaecrista fasciculata; *competition; fitness; native legume; partridge pea; range edge; recruitment; removal experiment.*

INTRODUCTION

Species' responses to environmental change include changes in population abundance, adaptation, habitat shifts, and range shifts. However, predictions of how species will respond to contemporary climate change are overwhelmingly based on current climatic distributions, and given these, how ranges may shift. Projections of current species distributions into future climate scenarios suggest that many species are at risk of extinction due to loss of suitable climatic conditions, even with unlimited dispersal (Thomas et al. 2004). These predictions assume that species' distributions are primarily limited by climatic conditions (Pearson and Dawson 2003). The extent to which species' current distributions match their potential geographic distribution (i.e., range edge equilibrium) is unclear (Gaston 2003). Moreover, abiotic factors such as soil type and biotic factors such

as competitors and enemies are also important determinants of species' current distributions (i.e., the realized niche [Hutchinson 1957]).

Range edge equilibrium can be tested by examining the fitness of individuals within and beyond the species' current range using transplant common garden experiments. Finding that population growth rate is reduced below replacement ($\lambda < 1$) beyond a species' current range edge and $\lambda > 1$ within the range would indicate that the species is in range edge equilibrium. Empirical work has revealed that the fitness of a species decreases toward and beyond the range edge in some cases (Jenkins and Hoffman 1999, Angert and Schemske 2005, Griffith and Watson 2006) but not in others (Prince and Carter 1985, Norton et al. 2005, Marsico and Hellmann 2009, Samis and Eckert 2009). Further, recent estimates of rates at which tree species shift indicate that many species ranges may be limited by dispersal, and not by climate alone (Svenning and Skov 2007). This evidence, taken together, presents a challenge to the common assumption that species are in

equilibrium with their ranges (e.g., Haldane 1956, Kirkpatrick and Barton 1997, Case and Taper 2000).

Species may not be in demographic equilibrium with their climatic tolerance limits for a number of reasons, including dispersal barriers (Gilman 2006), low dispersal rates (Vellend et al. 2003, Marsico and Hellmann 2009), lack of suitable habitat (Prince and Carter 1985, Holt and Keitt 2000), or biotic interactions (Price and Kirkpatrick 2009). While the interplay of climate and biotic interactions was proposed to limit species' ranges since as early as Darwin (1859:174–176), and was considered to play a prominent role early in the 20th century (Griggs 1914, Grinnell 1917), the development of theoretical models of range limits including these interactions (Hochberg and Ives 1999, Case and Taper 2000, Case et al. 2005, Price and Kirkpatrick 2009) lagged behind models focusing on climate and gene flow alone (reviewed in Sexton et al. 2009). Similarly, empirical work on range limits has often ignored interacting species, or treated them as secondary factors that modulate the location of range limits without determining them (but see Loehle 1998, Gross and Price 2000, Harley 2003, Samis and Eckert 2009). Empirical work incorporating biotic interactions is necessary because the effects of interacting species may not be consistent across the range. For example, biotic interactions may change from competitive to facilitative at different geographic range locations, as predicted by the stress-gradient hypothesis (Bertness and Callaway 1994, Brooker et al. 2008, Maestre et al. 2009). Finally, if range edge conditions are stressful, interactions with enemies are more likely to reduce individual fitness (e.g., the plant stress hypothesis [White 1984]).

In this study, we evaluate the extent to which the native annual legume *Chamaecrista fasciculata* is in range edge equilibrium, given its climatic tolerances, at its northern and western range edges. To investigate this, we estimate individual lifetime fitness and population growth rate at common garden sites within and beyond the species' current range edge. Finding that individual fitness or population growth decreases below replacement across the range edge would indicate that *C. fasciculata* will not persist beyond the range edge. Further, we examine how biotic interactions modulate the potential for *C. fasciculata* to expand into climatically suitable regions. Specifically, we manipulate the presence of neighboring plants to examine their effect on plant fitness in both natural populations and experimental populations within and beyond the current range edge. Finding a significant negative effect of competitors on fitness at and beyond the range edge would imply that the distribution of *C. fasciculata* is limited not by climatic tolerance alone, but also by the interaction of climate and biotic factors.

MATERIALS AND METHODS

Chamaecrista fasciculata (partridge pea; Fabaceae) is an annual species native to North America with a large
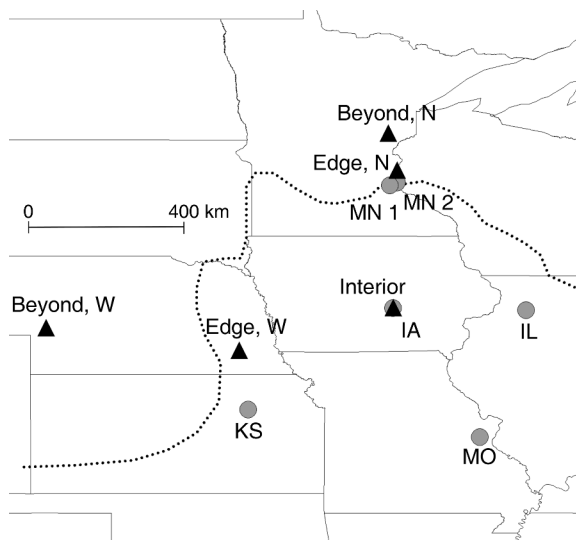

FIG. 1. Map of transplant sites (triangles) and seed source populations (circles). The dotted line is the approximate range edge of the native annual legume *Chamaecrista fasciculata* based on Biota of North America (BONAP) maps (Kartesz and Biota of North America Program 2011). Population abbreviations (by state) are: IL, Illinois; MO, Missouri; IA, Iowa; MN, Minnesota; KS, Kansas. Details of transplant and seed source sites are given in the Appendix: Tables A1 and A2.

geographic range from Mexico to north-central and eastern United States. The approximate northern range limit for this species runs from southern Minnesota east to Connecticut, and the western range limit is from western Minnesota south through Texas into Mexico (Kartesz and Biota of North America Program [BO-NAP] 2011). The northern and western range limits do not coincide with distinct geographical barriers; rather they follow isoclines of mean annual temperature and precipitation, respectively. Populations are found in old fields, open woodlands, disturbed prairies, and road-sides. *C. fasciculata* is insect pollinated and self-compatible, but highly out-crossing (Fenster 1991a). Seeds are explosively dispersed from the seedpods in the fall, typically reaching only a few meters from the plant (Fenster 1991a), and there is a limited seed bank, with >90% of the seeds that will germinate doing so in the first year (Fenster 1991b).

Natural populations: interannual fitness variation and the effect of neighbors at different range locations

In June 2007, we located four populations of *C. fasciculata* from its northern range edge in Minnesota south to Kansas: (1) Grey Cloud Dunes Scientific and Natural Area, Cottage Grove, Minnesota (MN 1), (2) Conard Environmental Research Area, Grinnell College, Kellogg, Iowa (IA), (3) Green River Wildlife Area, Harmon, Illinois (IL), and (4) Konza Prairie Biological Station, Kansas State University, Manhattan, Kansas (KS) (Fig. 1; Appendix: Table A1). Within each population, 30 pairs of plants within 50 cm of each

other were randomly selected, except at the IL site where only 10 pairs were selected because of small population size in this year. One plant in each pair was assigned at random to a neighbor removal treatment, and all aboveground vegetation within 20 cm of the plant was clipped at the beginning of the season (June) when seedlings were tagged, while the other plant was left unmanipulated with neighbors present. At the end of the growing season in late September and October, we returned to each site to record the number of seedpods produced by each plant. We repeated this experiment for the following two years, with sample sizes ranging from 20 to 40 pairs of plants depending on the site and year. In 2008, we added a population at Tyson Research Station annex (Washington University) in Eureka, Missouri (MO), and a second population at the range edge in Minnesota, Afton State Park (MN 2). Further, we collected data on total precipitation and average temperature during the growing season (1 May–30 September) for each year from the weather station nearest to each site; either a weather station on site (IA and KS) or the nearest airport weather station: IA, Conard Environmental Research Area weather station (data *available online*);[4] IL, KSQI, Whiteside Co. Airport, Sterling, Illinois (data *available online*);[5] KS, Konza Prairie Biological Station, weather data (*available online*);[6] MO, KSUS, Spirit of St. Louis airport (see footnote 5); MN 1/MN 2, KSGS, South St. Paul municipal airport (see footnote 5). We selected these climate variables because they are likely to be ecologically relevant (Etterson 2004) for the annual life history of this species. We also examined growing degree-days base 10°C (50°F), but found this was highly correlated ($r = 0.96$) with growing-season temperature, contributing little additional predictive capability.

Statistical analyses

To investigate the effect of range location and neighbor removal on fitness in natural populations, we used generalized linear models (GLMs) implemented in the MASS library (Venables and Ripley 2002, Crawley 2007) in R (R Development Core Team 2009). We fit GLMs with seedpod production as the dependent variable, and site, year, neighbor treatment (removed or present) and all interactions as predictors. To account for overdispersion in the data, we fit with a quasi-Poisson distribution. Model selection was performed by sequentially dropping terms from the full model, starting with interactions, and testing the significance using the likelihood ratio test (LRT). Further, we examined the relationship between growing-season temperature, precipitation, and seedpod production as the correlation

between seedpods produced and growing-season (May–October) temperature or precipitation.

Experimental populations: fitness and biotic interactions within and beyond the range

We collected seed in September and October 2008 from haphazardly selected plants (maternal families) at least 3 m apart in all of the populations studied above, except for MN 2 due to small population size. In April and May 2009, we established experimental populations at five sites: (1) one within the range (Interior), (2 and 3) one near each of the northern (Edge, N) and western (Edge, W) range edges, and (4 and 5) one beyond (Beyond, N; Beyond, W) each of these range edges (Fig. 1). The north and west edge sites were located orthogonally from the interior site, near the edge of *C. fasciculata*'s range (Fig. 1), along gradients of mean annual temperature (MAT) and annual precipitation (PPT), respectively (Hijmans et al. 2005, WorldClim data, 1960–1990 average [Appendix: Table A2]). From the Interior site to the Beyond, W site, annual precipitation decreases by 420 mm, while mean annual temperature increases by only 0.4°C. From the Interior to Beyond, N site, mean annual temperature decreases by 5.2°C and annual precipitation decreases by 190 mm, but soil water availability may not be greatly affected because the lower temperatures reduce evapotranspiration (Kemper and Corey 1994). The interior and edge sites were selected because *C. fasciculata* was found nearby, but not at the site, while the beyond-edge sites were placed in suitable habitats (i.e., open fields) 150–300 km beyond the recorded range limit of *C. fasciculata*. All sites were chosen to have loam soils, as soil type can influence fitness (Stanton-Geddes 2011).

We planted four seeds from each of 40 maternal families from each population at the interior and edge sites ($n = 800$ seeds total), and, due to seed limitation, two seeds from each maternal family in each treatment at the beyond-edge sites ($n = 400$ seeds total). The seeds were planted in 10 blocks of either 20 (interior and edge) or 10 (beyond edge) plots, each consisting of four seeds randomly selected from a single family and planted in a circular pattern with a diameter of 20 cm (Fig. 2). The plots were separated by 50 cm from each other. We expected that most seeds dispersing from these plants would fall within this distance, as >80% of seeds are reported to land within 0.5 m of the parent plant in natural settings (Fenster 1991a). One control plot with no seed additions was included in each block as a basis for evaluating potential recruitment from the seed bank. We began planting at southern sites and proceeded north to track natural timing of germination. Seeds were sterilized with 10% sodium hypochlorite (NaOCl) and scarified with a metal file prior to planting. Dried vegetation from the previous year was removed prior to planting. Otherwise sites were unmanipulated so that dispersing seeds would encounter natural conditions.

FIG. 2. Diagram of experimental design at each transplant site. Ten blocks were haphazardly located at each site. Within each block, either 20 (interior and edge sites) or 10 (beyond-edge sites) plots were regularly spaced 120 cm from each other in 3–5 rows. Rows were staggered such that all plots had a 60 cm radius surrounding area. Each plot was planted with four seeds from the same source population of *C. fasciculata*, with seeds placed 10 cm from the center of the plot in each cardinal direction. Each plot was randomly assigned to one of two treatments: neighbor removal or unmanipulated (neighbors present).
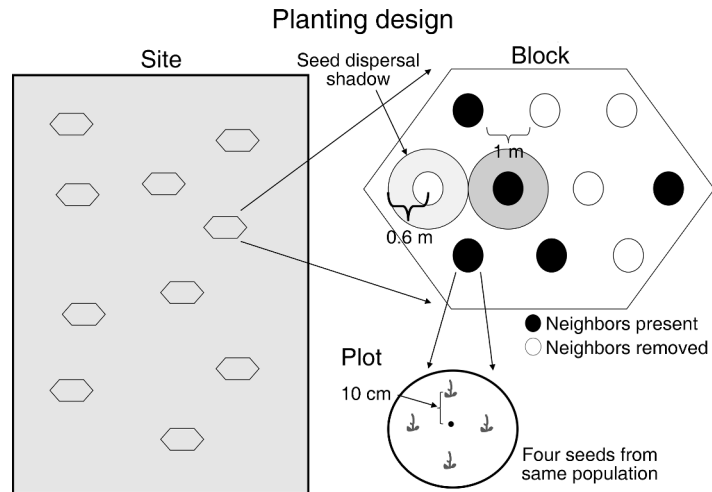
Each plot was randomly assigned to one of two treatments, neighbor removal or unmanipulated with neighbors present. The neighbor removal treatment was imposed by spraying glyphosate (Roundup, Monsanto, St. Louis, Missouri, USA) on all vegetation within the 0.6 m radius circle surrounding each neighbor removal plot 24 hours prior to planting, and clipping vegetation immediately before planting. Neighbor removal treatments had significantly more bare ground than neighbors present ($F_{1, 687} = 803$, $P < 0.0001$) when early-season measurements were taken, and this varied by site, ranging from 57% more at the interior site to 195% more at the north edge site ($F_{4, 683} = 49.5$, $P < 0.0001$).

Approximately four weeks after planting we recorded early-season survival. During the middle of the growing season in July, we recorded survival, and at the end of the growing season in late September and early October after plants had senesced, we recorded survival and the number of seedpods produced by each plant. To calculate population growth rate across an entire generation, from the number of seedlings in 2009 to the number of seedlings in 2010, we returned to each site the following June, after natural germination. We searched exhaustively within 0.6 m of the center of each plot (Fig. 2). *C. fasciculata* seedlings had two to four leaves at this time and were easily visible. As no *C. fasciculata* plants were in the immediate area of each experimental population and we found no seedlings outside the blocks at each site, all the seedlings found were assumed to be from experimental plants in the previous year.

Statistical analyses

To determine the effects of geographic range, source population, and competitors on fitness, we modeled lifetime fitness for each individual using aster models (Geyer et al. 2007, Shaw et al. 2008) in R (R Development Core Team 2009), which allow unified analysis of multiple life history stages with appropriate statistical distributions. Our aster model integrated four life history stages; early-season survival, fall survival, whether a plant produced seedpods, and the number of seedpods produced (Appendix: Fig. A1a). For the number of seedpods, we used a zero-truncated negative binomial because the data had a long right tail. We fit aster models with fixed effects for site, population, competition treatment, and all interactions. We tested whether each interaction improved the fit of the model to the data using LRTs comparing submodels to the full model. Finding a significant site × treatment interaction would suggest that the effect of competitors varies by geographic region.

To investigate at which life history stages each factor affected fitness, we performed stepwise forward model comparison beginning with a model that included each main effect at the final fitness stage (e.g., seedpods). We added a term for each main effect specified at each previous life history stage and used LRTs to evaluate whether the term was significant. Stepwise forward model building was performed to avoid selecting over-parameterized models. To test for intrasite environmental heterogeneity, we also tested the effect of blocks nested within site. The current aster package only accommodates single-parameter exponential family distributions, so the size parameter for the negative-binomial distribution for seedpods was determined by fitting a negative binomial distribution (fitdistr in the library MASS [Venables and Ripley 2002]) to the conditional distribution of the seedpod data. Goodness of fit of the negative binomial distribution for seedpods was confirmed by the Pearson residuals having approximately a mean of zero and a variance of one with few outliers (Shaw et al. 2007: Section 3.7). Predicted values for each life history stage at each site were obtained using parameter estimates from the best-fitting aster model. Variances for these estimates were calculated assuming that they were asymptotically normally distributed (Geyer et al. 2007). Parametric bootstraps

of our data support the use of these assumptions for our analyses (not shown).

We estimated population growth rate in two ways to set upper and lower bounds on the true value because seedling recruitment into control plots and plots without any surviving parents in the previous year was greater than anticipated (~30%). First, we ignored the plot design, and calculated population growth at the level of each site by summing the number of seeds germinated in 2009 and the number of seedlings found in 2010, and calculated population growth rate as λ = (number seedlings in 2010)/(number seedlings in 2009). To account for the fact that 21% of each block was unsearched because we only searched within a 60 cm diameter of each plot (Fig. 2), we estimated the number of unobserved seedlings in each block by assuming that the density of seedlings in the unsearched area was the same as within the searched area. This sets an upper bound on our estimate of population growth rate at each site. Our population growth estimates are similar to measurements of the finite rate of population increase (Norton et al. 2005), as we planted at low density in natural settings, and thus should give reasonable approximations of the potential for population growth after colonization. This estimate of population growth is not sensitive to assignment of seedlings to parents, but it does not allow us to account for differences among treatments.

To estimate the lower bound λ, population growth rate for each competition treatment, we modeled λ at the level of each plot using aster models (Appendix: Fig. A1b). By analyzing plot records from seeds planted in 2009 to seedlings recruited in 2010, this aster model takes into account mortality from seed predators and winter conditions as well as differences in survival and reproduction in 2009. Seedlings that were found in empty plots (i.e., those that did not have reproductive plants in the previous fall and control plots) could not be definitively associated with their parents and so were ignored in this analysis. While a few seedlings in any plot may have originated from a different parent, these are likely far fewer than seedlings that dispersed away from that plot and were therefore not counted, which likely underestimates plot-level seedling production (lower bound for λ). We tested fixed effects of block, site, competition treatment, and the interaction of site and treatment as before. Finally, we calculated population growth rate from the aster model as the predicted number of seedlings in 2010 divided by the predicted number of seedlings in 2009 for each treatment combination, and calculated confidence intervals by the delta method (Geyer and Shaw 2010).

RESULTS

Natural populations: interannual fitness and the effect of neighbors at different range locations

In natural populations, overall seedpod production was greatest at the southern sites and lower at northern sites (Fig. 3). However, there was significant interannual variation (Table 1) such that this pattern varied among years. In 2008 seed production steadily decreased toward the northern range edge (Fig. 3a). By contrast, in 2009, seed production was greatest at a northern-edge site (MN 1) and low at the southern-most site (MO). Neighbor removal significantly increased seedpod production at all sites, with similar effects at the different sites (Fig. 3b, Table 1). Growing-season precipitation and the average number of seedpods produced by individuals at each site correlated positively but weakly over the three years of the experiment ($r = 0.38$, $P = 0.17$; Appendix: Table A3). Greater seedpod production in years with higher rainfall at the southern sites (MO, KS, and IL; Appendix: Table A3; Fig. 3a) strongly influenced this relationship. We detected no evidence that growing-season temperature affected seedpod production ($r = 0.20$, $P = 0.50$).

Experimental populations: fitness and biotic interactions within and beyond the range

Lifetime seedpod production of experimental populations was reduced to zero or nearly so beyond both the western and northern range edges, indicating that even with dispersal, the current genetic composition of the study population does not allow range expansion (Table 2, Fig. 4). The fitness components underlying the decline in fitness beyond the northern and western range edges differed. Beyond the western edge, early-season survival was low, as was the number of seedpods produced given that a plant survived and produced any pods (Fig. 4). However, beyond the northern edge, early-season survival was high, but the probability of a plant surviving to the end of the season was low, and very few plants that survived produced any pods.

Source population only had a significant effect on early-season survival, with the IA population having greatest early-season survival at four of five sites, while the KS population had lowest early-season survival at three of five sites. The largely consistent effect of seed source on early-season survival could arise from influences of maternal environment in the source locations on survival, e.g., through differences in seed provisioning. Lifetime seedpod production (i.e., taking variation in survival into account) did not differ significantly among populations (Table 2), indicating that fitness differences reflected in early-season survival diminished across the season. This was due, in part, to low overall survival and reproduction; only 11–22 individuals of the 80 individuals of each population survived to produce seeds at the interior site, and fewer at the remaining sites.

The effect of the neighbor removal treatment varied with life history stage. Consistent with the results in natural populations, neighbor removal significantly increased seedpod production, given survival, at all sites except the Beyond, N site where no plants survived in the neighbor removal treatment (Fig. 4, Table 2). However, neighbor

FIG. 3. Predicted values (mean ± SE) from the best-fit generalized linear models of the number of seedpods produced per *C. fasciculata* plant (a) across three years (2007–2009) in six natural populations at different geographic range locations (see Fig. 1), and (b) the effect of neighbor removal (black bars, neighbors present; white bars, neighbors removed) at these sites, averaged across the years. Abbreviation: n.d. indicates no data.
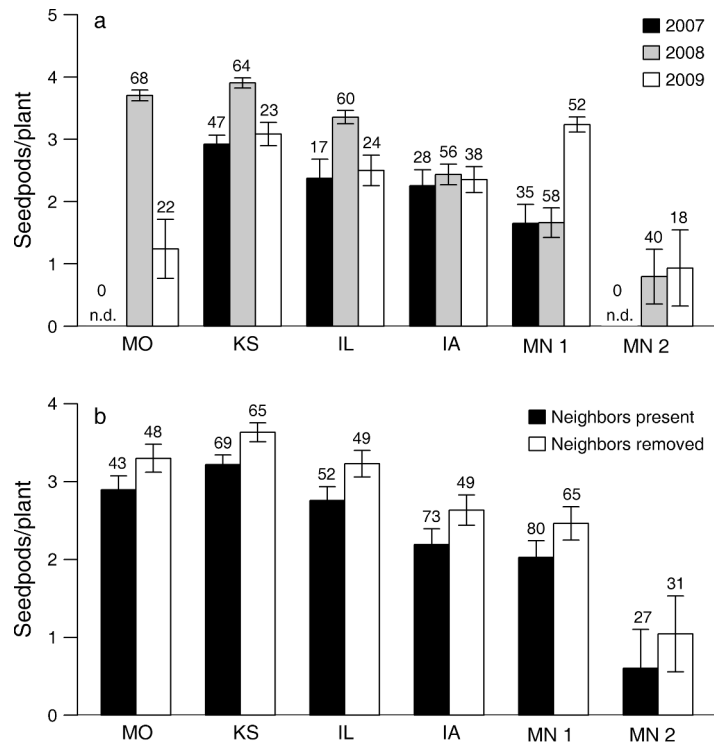
removal reduced early-season survival (Table 2) everywhere except the Edge, N site (Fig. 4). The positive effect of neighbors on early-season survival was large enough for lifetime fitness to be greater in the neighbor present than the neighbor removal treatment at the Edge, W and Interior sites (Fig. 4).

Population growth rate tracked the overall pattern of fitness in the previous year, with greatest population growth at the interior site, intermediate population growth at the edge sites, and zero population growth at both beyond-edge sites (Table 3). As expected, the aster estimates of λ based on experimental subpopulations were generally lower than the overall λ at the site level because they did not account for seedlings that may have dispersed outside of plots, but in general, both methods gave qualitatively similar results (Table 3). Contrasting with the results for seedpod production, λ was greater in the neighbor removal than the neighbor present treatment at the Edge, W site (Table 3). This result

was due to an exceptionally large number of seedlings (43 compared to an average of 2.3 in other plots) found in one neighbor removal plot that contained one parent with 50 seedpods in the previous generation. If the data is reanalyzed with the number of seedlings in this patch changed to the site average, the confidence intervals for population growth rate between treatments completely overlap, indicating that this result should be interpreted with caution. Interestingly, even at the Interior site, where a large and stable population has been present for many years, estimates of the confidence interval for population growth rate included values that were below the replacement rate ($\lambda < 1$).

DISCUSSION

Our results show that population growth rate of a widespread annual species decreases to near zero beyond its western and northern range edges, indicating that it is in demographic equilibrium at these range limits. We

TABLE 1. Summary of generalized linear model comparisons to test for the effects of site, year, competition treatment, and all interactions on the number of seedpods produced per plant in six natural populations of *Chamaecrista fasciculata* across three years.

Term	Residual df	Test df	Deviance	F	P
Year × site × treatment	619	8	45.9	0.32	0.96
Site × treatment	627	5	49.7	0.57	0.73
Year × treatment	632	2	3.1	0.09	0.91
Year × site	634	8	2296.7	16.5	<0.0001
Treatment	642	1	620.2	27.3	<0.0001
Year	642	2	1199.8	26.4	<0.0001
Site	642	5	4231.1	37.2	<0.0001

TABLE 2. Summary of results from aster model comparisons testing the effects of transplant site (site), source population (population), competition treatment (treatment), and their interactions on individual fitness.

Term	Residual df	Test df	Deviance	P
Full	82			
Block	37	45	157.6	<0.0001
Treatment × population	78	4	6.2	0.18
Site × population	62	16	31.1	0.013
Site × treatment	74	4	43.5	<0.0001
Main effects only	13			
Treatment	12	1	0.31	0.58
Population	8	4	3.81	0.43
Site	4	4	61.70	<0.0001
Life history effects above and beyond main effects				
Base	13			
Site@early-season survival	17	4	350.0	<0.0001
Site@fall survival	21	4	325.3	<0.0001
Site@anypods	25	4	52.6	<0.0001
Population@early-season survival	29	4	17.8	0.001
Population@fall survival	33	4	5.5	0.24
Population@anypods	33	4	7.5	0.11
Treatment@early-season survival	30	1	102.0	<0.0001
Treatment@fall survival	31	1	0.81	0.37
Treatment@anypods	32	1	9.4	0.002

Notes: The effect of block and the interactions were tested against the full model. The effect of the predictors at each life history stage was tested by adding them to the "Base" model including the effect of site, population, and treatment specified at ("@") the fitness level of seedpods. "Anypods" is the probability of producing seedpods. Thus these models are testing the significance of each predictor at each life history stage above and beyond its effect on lifetime fitness.

emphasize that this pattern of a decline in fitness beyond the range edge is supported by both estimates of individual fitness and population growth rate, accounting for recruitment into the next generation, in experimental populations. Further, we demonstrate multifaceted effects of interacting species. While neighboring plants reduce reproduction, they enhance early-season survival. Thus, if early-season survival is critical for population establishment, as our results suggest for *C. fasciculata*, then neighboring plants may facilitate range expansion.

Causes of abrupt range limits

The experiment demonstrated abrupt declines in fitness beyond both range edges (Fig. 4), such that, for our study populations, these sites can be regarded as demographic sinks. Similarly, under natural conditions of neighbors present, fitness at the northern range edge was near zero, although it was enhanced in the neighbor removal treatment (Fig. 3). At the western range edge, however, fitness in the natural populations was similar to that of the interior sites (Fig. 3). This maintenance of fitness at the range edge may be due to adaptation of peripheral populations to their local conditions (Kawecki 2008). Though we did not find evidence for local adaptation in this study, potentially due to limited sample size, previous work indicates that populations of *C. fasciculata* are locally adapted on a geographic scale similar to this, including the Konza Prairie population near the western range edge (Galloway and Fenster 2000, Etterson 2004, Stanton-

Geddes 2011). The abrupt decline of fitness beyond the range edge may reflect that populations have not had the opportunity to establish in and adapt to these conditions, that they lack the genetic variation to do so, or they are prevented from adapting by asymmetric gene flow from larger interior populations. This final hypothesis is unlikely to contribute, as we found no evidence for gene flow from interior to edge populations in a companion study (Stanton-Geddes 2011).

The decline of fitness at the northern edge compared to the range interior (Figs. 3 and 4) may be due to bottlenecks associated with northward range expansion limiting adaptation of populations to these conditions (Stanton-Geddes 2011). Nevertheless, fitness remains relatively high at the range edges, though not beyond them, as seen in other experimental work. For example, populations of the annual plant *Xanthium strumarium* at its northern range edge maintained fitness equal to interior populations by adaptation to reproduce earlier (Griffith and Watson 2005), but transplants beyond the range edge completely failed to reproduce (Griffith and Watson 2006).

The abrupt decline in fitness beyond the range could be due to multiple interacting factors that determine the range edge. For example, in a companion study at these sites, we found that suitable rhizobia were nearly absent beyond the range edge, and that plant growth depended strongly on rhizobia availability (Stanton-Geddes and Anderson 2011). This suggests that the difference in climate conditions coupled with the paucity of rhizobia,
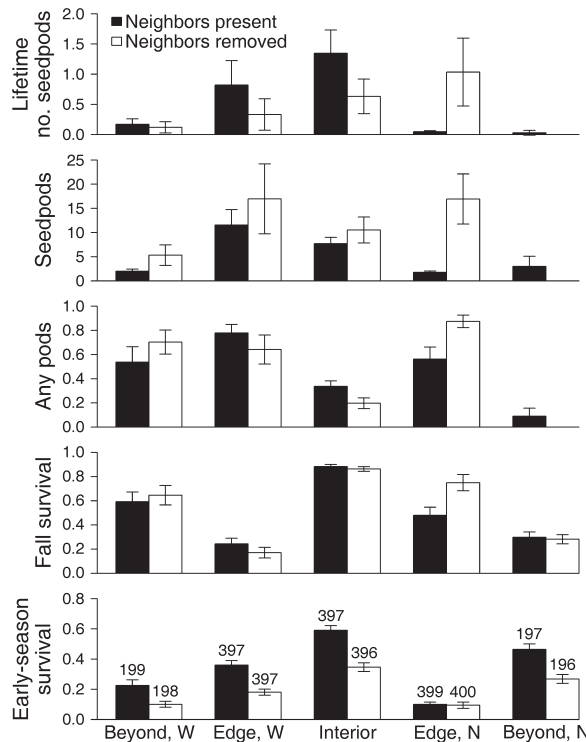
FIG. 4.   Predicted values (mean ± SE) from the best-fit aster model of overall lifetime seedpod production and its underlying components (seedpods produced given survival ["Seedpods"], the probability of a plant producing any pods, fall survival, and early-season survival) for *C. fasciculata* transplanted into sites within the Interior, at the western range edge (Edge, W), at the northern range edge (Edge, N) and beyond these range edges (Beyond, W; Beyond, N). Sample sizes above bars in the lower panel also apply for measurements in all other panels.

potentially mediated through a negative feedback with the absence of *C. fasciculata*, may together account for the range edge.

Biotic interactions

The finding of increased lifetime seedpod production in the presence of neighbors compared to the neighbor removal treatment, mediated through greater early-season survival (Fig. 4), was surprising given that the effect of neighbors at range limits is expected to be competitive (Darwin 1859, Case and Taper 2000, Price and Kirkpatrick 2009). Facilitation is typically described in stressful environments, such as alpine habitats (Callaway et al. 2002). Our results suggest that this facilitative effect of neighbors can occur in favorable habitats at stressful life history stages, such as seedling survival. Two related mechanisms could explain the facilitative effect of neighbors. First, in arid environments, perennial shrubs act as "nurse plants" by providing shade for annual seedlings while they grow and develop their own root zones (Went 1942, Brooker et al. 2008). Second, neighboring perennial plants with deep root zones may increase soil moisture by hydraulic lift, the passive movement of water through roots from deep to shallow soils (Caldwell et al. 1998). The perennial bunchgrasses that often co-occur with *C. fasciculata* could provide both of these benefits. Similar to our results, Marsico and Hellmann (2009) report that germination of three long-lived perennial *Lomatium* species transferred beyond their range on Vancouver Island was greater in the presence of neighboring vegetation. If early survival is the key stage for viable population establishment, neighbors may actually facilitate range expansion in some habitats.

In contrast to the other sites, neighbor removal increased early-season survival and lifetime fitness at the Edge, N site. Two factors related to this site likely explain this observation. First, 2009 was an exceptionally dry year at the north edge, so competition for moisture was especially strong at this site as shown by the overall low survival rates (Fig. 4). Second, this site was dominated by weedy herbaceous plants (53% herbaceous cover in the neighbor present treatment), and had relatively few grasses (16% at this site compared to 57% average at the other sites). Thus, it is likely that there was greater niche overlap between *C. fasciculata* and neighbors at this site, leading to greater competition for the already limited water resources and reducing any potential benefits of hydraulic lift. Similarly, Carter and Prince (1985) found that another annual ruderal species,

TABLE 3.   Confidence intervals (95%) for population growth rates at each site.

Site	Site λ	Aster λ	
		Neighbors present	Neighbors removed
Beyond, W	−0.01 to 0.03	−0.03 to 0.07	0
Edge, W	−0.17 to 1.19	0.11 to 0.44	0.23 to 0.70
Interior	0.47 to 1.42	0.52 to 1.29	0.27 to 0.78
Edge, N	−0.03 to 1.40	0	0.10 to 0.41
Beyond, N	0	0	0

Notes: The first data column is the overall site 95% CI for population growth rate calculated from the total number of seedlings in 2009 and 2010, accounting for unobserved seedlings in 2010. The second and third columns give the 95% CI for aster estimates of population growth rate. With the aster estimates, the effect of neighbors present can be compared to neighbors removed, but because unobserved seedlings are not included, these are probably underestimates. Negative estimates of λ occur because we did not truncate the confidence intervals at zero.

Lactuca serriola, did not coexist with other competitive ruderals near its range edge. This indicates that the effects of neighbors on individual fitness at and beyond the range edge will depend on neighbor identity.

Other biotic interactions that may influence fitness at different range locations include herbivory (Geber and Eckhart 2005). Browsing from herbivores, primarily deer, was greatest at the Interior site (percentage of plants browsed: Interior 72%; Edge, W 56%; Edge, N 19%; Beyond, W 0%; Beyond, N 23%; GLM deviance = 242, $P < 0.0001$), and the Interior was the only site where browsing had a significant negative effect on fitness (Appendix: Table A4). This may be because there were more deer at this site, there were fewer attractive co-occurring plants, or because *C. fasciculata* plants were taller and more apparent to herbivores at this site than the other sites. The negative effect of browsing on fitness is likely partially responsible for the low population growth rate at this site.

In summary, our results show that the absolute fitness of *C. fasciculata* transplanted beyond the range edge is near zero, precluding establishment of populations in these regions. This reduction in fitness may be caused by the direct effect of climate, or more likely, the impact of climate and biotic interactions. Moreover, our results suggest that ecological–genetic factors hinder adaptation to conditions beyond the range edge. Thus, even for a species currently in demographic equilibrium with its range limits, range shifts in response to climate change will depend not only on dispersal, but also on the rate of adaptation and the community of interacting species. These results underscore the conclusion of Pearson and Dawson (2003) that bioclimatic envelopes can only be used as a "first approximation" of species' future distributions. The development of more advanced models (Pagel and Schurr 2011) will improve scientists and managers ability to predict species' range shifts. However, as evidence accumulates that species respond independently to climate change (Davis et al. 2005, Lavergne et al. 2010) and that plant community composition lags behind climate change (Bertrand et al. 2011), the predictive ability of these models remains uncertain.

LITERATURE CITED

Angert, A., and D. Schemske. 2005. The evolution of species' distributions: reciprocal transplants across the elevation ranges of *Mimulus cardinalis* and *M. lewisii*. Evolution 59:1671–1684.

Bertness, M. D., and R. M. Callaway. 1994. Positive interactions in communities. Trends in Ecology and Evolution 9:191–193.

Bertrand, R., J. Lenoir, C. Piedallu, G. Riofrío-Dillon, P. de Ruffray, C. Vidal, J.-C. Pierrat, and J.-C. Gégout. 2011. Changes in plant community composition lag behind climate warming in lowland forests. Nature 479:517–520.

Brooker, R. W., et al. 2008. Facilitation in plant communities: the past, the present, and the future. Journal of Ecology 96:18–34.

Caldwell, M. M., T. E. Dawson, and J. H. Richards. 1998. Hydraulic lift: consequences of water efflux from the roots of plants. Oecologia 113:151–161.

Callaway, R. M., et al. 2002. Positive interactions among plants increase with stress. Nature 417:844–848.

Carter, R. N., and S. D. Prince. 1985. The geographical distribution of prickly lettuce (*Lactuca serriola*): I. A general survey of its habitats and performance in Britain. Journal of Ecology 73:27–38.

Case, T., and M. Taper. 2000. Interspecific competition, environmental gradients, gene flow, and the coevolution of species' borders. American Naturalist 155:583–605.

Case, T. J., R. D. Holt, M. A. McPeek, and T. H. Keitt. 2005. The community context of species' borders: ecological and evolutionary perspectives. Oikos 108:28–46.

Crawley, M. J. 2007. The R book. John Wiley and Sons, Chichester, UK.

Darwin, C. 1859. On the origin of species by means of natural selection, or the preservation of favoured races in the struggle for life. John Murray, London, UK.

Davis, M. B., R. G. Shaw, and J. R. Etterson. 2005. Evolutionary response to changing climate. Ecology 86:1704–1714.

Etterson, J. R. 2004. Evolutionary potential of *Chamaecrista fasciculata* in relation to climate change. I. Clinal patterns of selection along an environmental gradient in the Great Plains. Evolution 58:1446–1458.

Fenster, C. 1991a. Gene flow in *Chamaecrista fasciculata* (Leguminosae) I. Gene dispersal. Evolution 45:398–409.

Fenster, C. B. 1991b. Gene flow in *Chamaecrista fasciculata* (Leguminosae) II. Gene establishment. Evolution 410–422.

Galloway, L. F., and C. Fenster. 2000. Population differentiation in an annual legume: local adaptation. Evolution 54:1173–1181.

Gaston, K. J. 2003. The structure and dynamics of geographic ranges. Oxford University Press, Oxford, UK.

Geber, M. A., and V. M. Eckhart. 2005. Experimental studies of adaptation in *Clarkia xantiana*. II. Fitness variation across a subspecies border. Evolution 59:521–533.

Geyer, C. J., and R. G. Shaw. 2010. Aster models and Lande-Arnold beta, Technical Report 675. School of Statistics, University of Minnesota, Minneapolis, Minnesota, USA. http://purl.umn.edu/56394

Geyer, C. J., S. Wagenius, and R. G. Shaw. 2007. Aster models for life history analysis. Biometrika 94:415–426.

Gilman, S. E. 2006. The northern geographic limit of the intertidal limpet *Collisella scabra*: a test of performance, recruitment, and temperature hypotheses. Ecography 29:709–720.

Griffith, T. M., and M. A. Watson. 2005. Stress avoidance in a common annual: reproductive timing is important for local adaptation and geographic distribution. Journal of Evolutionary Biology 18:1601–1612.

Griffith, T. M., and M. A. Watson. 2006. Is evolution necessary for range expansion? Manipulating reproductive timing of a

weedy annual transplanted beyond its range. American Naturalist 167:153–164.

Griggs, R. F. 1914. Observations on the behavior of some species at the edges of their ranges. Bulletin of the Torrey Botanical Club 41:25–49.

Grinnell, J. 1917. The niche-relationships of the California Thrasher. The Auk 34:427–433.

Gross, S., and T. D. Price. 2000. Determinants of the northern and southern range limits of a warbler. Journal of Biogeography 27:869–878.

Haldane, J. B. 1956. The relation between density regulation and natural selection. Proceedings of the Royal Society of London B 145:306–308.

Harley, C. D. G. 2003. Abiotic stress and herbivory interact to set range limits across a two-dimensional stress gradient. Ecology 84:1477–1488.

Hijmans, R. J., S. E. Cameron, J. L. Parra, P. G. Jones, and A. Jarvis. 2005. Very high resolution interpolated climate surfaces for global land areas. International Journal of Climatology 25:1965–1978.

Hochberg, M. E., and A. R. Ives. 1999. Can natural enemies enforce geographical range limits? Ecography 22:268–276.

Holt, R. D., and T. H. Keitt. 2000. Alternative causes for range limits: a metapopulation perspective. Ecology Letters 3:41–47.

Hutchinson, G. E. 1957. Some concluding remarks. Cold Spring Harbor Symposium on Quantitative Biology 22:415–427.

Jenkins, N. L., and A. A. Hoffman. 1999. Limits to the southern border of *Drosophila serrata*: cold resistance, heritable variation, and trade-offs. Evolution 53:1823–1834.

Kartesz, J. T., and Biota of North America Program (BONAP). 2011. North American Plant Atlas. Biota of North America Program, Chapel Hill, North Carolina, USA. http://www.bonap.org

Kawecki, T. J. 2008. Adaptation to marginal habitats. Annual Review of Ecology, Evolution, and Systematics 39:321–342.

Kemper, W., and A. Corey. 1994. Accumulation of water in soils under gravel and sand mulches. Soil Science Society of America Journal 58:56.

Kirkpatrick, M., and N. Barton. 1997. Evolution of a species' range. American Naturalist 150:1–23.

Lavergne, S., N. Mouquet, W. Thuiller, and O. Ronce. 2010. Biodiversity and climate change: integrating evolutionary and ecological responses of species and communities. Annual Review of Ecology, Evolution, and Systematics 41:321–350.

Loehle, C. 1998. Height growth rate tradeoffs determine northern and southern range limits for trees. Journal of Biogeography 25:735–742.

Maestre, F. T., R. M. Callaway, F. Valladares, and C. J. Lortie. 2009. Refining the stress-gradient hypothesis for competition and facilitation in plant communities. Journal of Ecology 97:199–205.

Marsico, T. D., and J. J. Hellmann. 2009. Dispersal limitation inferred from an experimental translocation of *Lomatium* (Apiaceae) species outside their geographic ranges. Oikos 118:1783–1792.

Norton, L. R., L. G. Firbank, A. Scott, and A. R. Watkinson. 2005. Characterising spatial and temporal variation in the finite rate of population increase across the northern range boundary of the annual grass *Vulpia fasciculata*. Oecologia 144:407–415.

Pagel, J., and F. M. Schurr. 2011. Forecasting species ranges by statistical estimation of ecological niches and spatial population dynamics. Global Ecology and Biogeography 21:293–304.

Pearson, R. G., and T. E. Dawson. 2003. Predicting the impacts of climate change on the distribution of species: are bioclimate envelope models useful? Global Ecology and Biogeography 12:361–371.

Price, T. D., and M. Kirkpatrick. 2009. Evolutionarily stable range limits set by interspecific competition. Proceedings of the Royal Society B 276:1429.

Prince, S. D., and R. N. Carter. 1985. The geographical distribution of prickly lettuce (*Lactuca serriola*): III. Its performance in transplant sites beyond its distribution limit in Britain. Journal of Ecology 73:49–64.

R Development Core Team. 2009. R: a language and environment for statistical computing. 2.10. R Foundation for Statistical Computing, Vienna, Austria.

Samis, K. E., and C. G. Eckert. 2009. Ecological correlates of fitness across the northern geographic range limit of a Pacific Coast dune plant. Ecology 90:3051–3061.

Sexton, J. P., P. J. McIntyre, A. L. Angert, and K. J. Rice. 2009. Evolution and ecology of species range limits. Annual Review of Ecology, Evolution, and Systematics 40:415–436.

Shaw, R. G., C. J. Geyer, S. Wagenius, H. H. Hangelbroek, and J. R. Etterson. 2007. Supporting data analysis for "Unifying life history analyses for inference of fitness and population growth" Technical Report 658. School of Statistics, University of Minnesota, Minneapolis, Minnesota, USA.

Shaw, R. G., C. J. Geyer, S. Wagenius, H. H. Hangelbroek, and J. R. Etterson. 2008. Unifying life-history analyses for inference of fitness and population growth. American Naturalist 172:E35–E47.

Stanton-Geddes, J. 2011. Limits to range expansion in the native annual legume *Chamaecrista fasciculata*. Dissertation. University of Minnesota, St. Paul, Minnesota, USA.

Stanton-Geddes, J., and C. G. Anderson. 2011. Does a facultative mutualism limit species range expansion? Oecologia 167:149–155.

Svenning, J. C., and F. Skov. 2007. Could the tree diversity pattern in Europe be generated by postglacial dispersal limitation? Ecology Letters 10:453–460.

Thomas, C. D., et al. 2004. Extinction risk from climate change. Nature 427:145–148.

Vellend, M., J. A. Myers, S. Gardescu, and P. Marks. 2003. Dispersal of *Trillium* seeds by deer: implications for long-distance migration of forest herbs. Ecology 84:1067–1072.

Venables, W. N., and B. D. Ripley. 2002. Modern applied statistics with S. Fourth edition. Springer, New York, New York, USA.

Went, F. W. 1942. The dependence of certain annual plants on shrubs in southern California deserts. Bulletin of the Torrey Botanical Club 69:100–114.

White, T. C. R. 1984. The abundance of invertebrate herbivores in relation to the availability of nitrogen in stressed food plants. Oecologia 63:90–105.

SUPPLEMENTAL MATERIAL

Appendix

Supplementary tables containing population and transplant site information, and a figure of the life history stages included in the aster modeling (*Ecological Archives* E093-142-A1).

Data Availability

Data associated with this paper have been deposited in Dryad: http://dx.doi.org/10.5061/dryad.d2c619hd