Pushing the limit: experimental evidence of climate effects on plant range distributions

LAUREL PFEIFER-MEISTER,1,5 SCOTT D. BRIDGHAM,1,2 CHELSEA J. LITTLE,3 LORIEN L. REYNOLDS,1 MAYA E. GOKLANY,1 AND BART R. JOHNSON2,4

1Institute of Ecology and Evolution, University of Oregon, Eugene, Oregon 97403 USA
2Environmental Science Institute, University of Oregon, Eugene, Oregon 97403 USA
3Evolutionary Biology Center, Uppsala University, Uppsala 75236 Sweden
4Department of Landscape Architecture, University of Oregon, Eugene, Oregon 97403 USA

Abstract. Whether species will be extirpated in their current geographic ranges due to rapidly changing climate, and if so, whether they can avoid extinction by shifting their distributions are pressing questions for biodiversity conservation. However, forecasts of climate change impacts on species’ geographic distributions rarely incorporate a demographic understanding of species’ responses to climate. Because many biotic and abiotic factors at multiple scales control species’ range limits, experimentation is essential to establish underlying mechanisms. We used a manipulative climate change experiment embedded within a natural climate gradient to examine demographic responses of 12 prairie species with northern range limits within the Pacific Northwest, USA. During the first year, warming decreased recruitment of species even at the coolest edge of their current ranges, but this effect disappeared when they were moved poleward beyond their current ranges. This response was largely driven by differences in germination rates. Other vital rates responded in unique and sometimes opposing ways (survivorship vs. fitness) to species’ current ranges and climate change, and were mediated by indirect effects of climate on competition and nutrient availability. Our results demonstrate the importance of using regional-scale climate manipulations and the need for longer-term experiments on the demographic responses that control species’ distributions.

Key words: climate manipulation; demography; geographical distribution; mediterranean grassland; niche; Pacific Northwest, USA; prairie; precipitation; range shift; recruitment; species loss; warming.

INTRODUCTION

There is compelling evidence that many taxa have shifted, expanded, or contracted their ranges in the past 30 years concurrent with recent climate change (Parmesan and Yohe 2003, Hickling et al. 2006, Parmesan 2006, Rosenzweig et al. 2007, Kelly and Goulden 2008, Normand et al. 2009, Thomas 2010, Chen et al. 2011, Crimmins et al. 2011, VanDerWal et al. 2012). These shifts have been attributed largely to changes in temperature, and less commonly, precipitation regimes (Kelly and Goulden 2008, Crimmins et al. 2011, VanDerWal et al. 2012), but it is impossible to decouple climatic effects from those of other environmental changes without experimentation (Sexton et al. 2009). Moreover, forecasts of climate change effects on species’ ranges project high turnover rates in coming decades with many species going extinct (Thuiller et al. 2011), but data to test model assumptions are rare. Furthermore, demographic parameters may not respond uniformly or linearly to changes in climate (Doak and Morris 2010). However, the majority of empirical studies only examine a single parameter, and may miss many potential additive or compensatory effects (Gaston 2009). Despite these recognized needs, experiments that decouple the effects of climate on species’ distributions from other local factors are scarce (e.g., Gedan and Bertness 2009, De Frenne et al. 2011) because of the difficulties of manipulating climate at a regional scale across a diverse suite of species.

To address this need, we experimentally increased temperature and precipitation at three sites across a 520-km latitudinal gradient of prairies in the interior valleys of the Pacific Northwest (PNW), USA. Typically, scientists have examined climate change impacts either by experimentally manipulating one or more factors at a single site or by assessing trends across natural latitudinal or elevational gradients. Combining these two approaches allows for both the controlled, mechanistic understanding of experimental manipulations and the ability to parse out generalizable regional trends vs. those that are locally dependent (Dunne et al. 2004).

Prairies of the PNW have a mediterranean climate, characterized by mild, wet winters, and increasingly hot, dry summers from north (Csb climate zone, “warm summer”) to south (Csa climate zone, “hot summer”);
Mediterranean ecosystems are expected to be particularly vulnerable to climate change as they already have been significantly impacted by land-use change, habitat fragmentation, and species invasions (Sala et al. 2000). It is anticipated that these ecosystems will have larger proportional losses of biodiversity than other terrestrial biomes (Sala et al. 2000, Klausmeyer and Shaw 2009). Furthermore, the interaction between changes in temperature and precipitation in Mediterranean regions has resulted in multidirectional range shifts (VanDerWal et al. 2012), making it imperative to understand these interactive effects.

At each of the three sites, we increased plant canopy temperature by 3°C above ambient and precipitation by 20% above ambient year-round in a fully factorial design. These increases are similar to climate change predictions for the PNW over the next 80 years (Mote and Salathé 2010). To investigate climate impacts on species ranges, we seeded 12 native prairie plant species (representing a variety of functional groups) that have their northern range limit within the PNW. At each site, we planted the closest local population of each species (which required moving some species north of their current range) and monitored each successive demographic stage. First, we asked in what ways and to what extent do plant species’ responses to projected changes in temperature and precipitation differ near their current northern range limit in comparison to beyond this limit? Second, we assessed the sensitivity of different vital rates to the direct and interactive effects of climate change, range limits, and local resource controls.

Materials and Methods

Treatment implementation

Site characteristics are summarized in Appendix A. Prior to treatment implementation, all sites received herbicide application followed by mowing and raking during the summer of 2009. The 60 plots (3 sites × 4 treatments × 5 replicates; 3 m diameter, 7.1 m²) were seeded in December 2009 with a common mix of 19 non-range-limited native forb and grass species from local populations for each site. The most aggressive invasive species were weeded during the establishment phase, after which natural succession was allowed to occur. Precipitation treatments were initiated in spring 2010, and all heating treatments were initiated by fall 2010.

We achieved consistent 3°C canopy heating by modulating infrared radiation output from six overhead 2000-W infrared heaters (Kalglo Electronics, Bethlehem, Pennsylvania, USA) angled at 45° to the surface that were controlled by temperature in the control plots (Kimball et al. 2008). “Dummy” heaters were erected over the remaining plots to control for shading effects. Our experimental warming treatment is consistent with the average predicted warming of a multi-model ensemble of atmosphere–ocean general circulation models (AOGCMs) of 3.0°C by the 2080s in the PNW (Mote and Salathé 2010).

Precipitation was collected on polycarbonate sheets and stored in a cistern. We used a gauged hose to add the additional 20% precipitation within two weeks of when it fell, resulting in an increase of intense precipitation events, similar to what has been observed in the United States over the 20th century (Groisman et al. 2004) and is predicted to occur globally with future climate change (Meehl et al. 2007). AOGCMs predict, on average, small absolute changes in rainfall in the PNW, but many models predict an enhanced seasonal precipitation cycle, with increased rainfall during the normal rainy season of the late fall, winter, and spring months, and drier conditions in the already dry summer season (Mote and Salathé 2010). Thus, our treatments emulate the predictions for the PNW (Appendix B).

Species selection and seeding

We selected 12 native plant species (Appendix C) based upon the criteria that (1) each species must have a medium to high fidelity to upland prairies in the PNW, and (2) their current northern range limit is within the PNW (~41–50° latitude). We split these species into three “range groups” (four species each) based on the Level III Ecoregion (U.S. EPA 2011) of their current northern range limit, and refer to these groups as (1) Lowest Northern Limit (LNL, northern range limit ~41–43° N), (2) Intermediate Northern Limit (INL, northern range limit ~43–46° N), and (3) Highest Northern Limit (HNL, northern range limit ~46–50° N). Detailed information about species selection and range group assignments can be found in Appendix D.

For each site and species, we used seed from the closest local population that was available. For those species that were outside their current range at one or more of our sites, we used seed from the nearest population from which we could reliably obtain it. Seed was either wild collected or obtained from native plant nurseries growing first-generation progeny. In October–November 2010, we planted 200 seeds in each plot (eight random subplots of 50 cm², 25 seeds each) for every species (4000 seeds per species per site).

Demographics of range-limited species

Beginning January 2011, we regularly monitored the eight subplots for each species and measured the following vital rates: germination (the proportion of seeds that emerged), seedling survivorship (the proportion of seedlings surviving to the end of the growing season), recruitment (the product of germination and seedling survivorship), fitness as indicated by both plant size (for all species), and seed set (annuals only), and net reproductive rate, $R_0$ (annuals only, the product of recruitment and seed set). Germination rates may be underestimated to the extent there was fall germination and subsequent death prior to the first January count. We revisited each subplot every 2–3 weeks until seed set
or senescence occurred in June–August 2010. After germinants became established, we thinned plants to a maximum of five plants per subplot. At the end of the growing season, we collected the annuals, dried (60°C for 48 h) and weighed their biomass, and counted the seeds produced. To avoid destructively sampling the perennials, we created allometric relationships for each species at each site to estimate biomass using the thinned plants ($R^2$ ranged from 0.68 to 0.88). An allometric relationship was not established for *Perideridia oregana* because during the first year it allocates most of its growth belowground; thus, this species is excluded from any analysis of plant size. Because no perennials flowered in the first year, there was no seed production data for perennials.

**Statistical analyses**

For statistical analyses, we averaged the eight subplots and used the larger plot as our replicate unit for each species. For all analyses by range group, we $z$-transformed germination rates, survivorship, plant size, and seed set within each species, resulting in an equal weighting of every species. We performed a four-way factorial ANOVA on the $z$-transformed scores with range group, site, heat, and precipitation as fixed main effects. If there was a significant interaction between range groups, site, and the treatments, we ran individual ANOVAs within each site and Tukey’s post hoc tests for differences between sites. We also ran two a priori Helmert contrasts comparing species within vs. outside their current range. We further analyzed data by species for recruitment and net reproductive rate, $R_0$ (annuals only), using ANOVAs to test for treatment effects within each site. For cases where the assumption of homogeneity of variance was violated, we used the nonparametric Kruskall–Wallis Test.

**RESULTS AND DISCUSSION**

Under ambient conditions at each site, species planted within their current range had higher recruitment than those outside their range (unhatched bars in Fig. 1), although all species were able to grow at each site. At the southern site, where each range group occurs naturally, there were no significant differences in recruitment among range groups (post hoc comparison, $P > 0.20$). At the central site, recruitment was approximately twice as high for the species planted inside their current range vs. those outside (a priori contrast, LNL vs. INL and HNL, $P = 0.05$). This was even more pronounced at our northern site, where species inside their range were 25 times more likely to successfully recruit than those outside their range under ambient conditions (a priori contrast, HNL vs. LNL and INL, $P < 0.001$).

Whether a species was found within or beyond its current range was an important determinant of how it responded to the climate treatments (range group × site × heat interaction, $P = 0.004$; Appendix E). When species were planted within their current range, increased temperature significantly decreased recruitment with the exception of one range group at one site (although the trend was consistent; Fig. 1; Appendices E and F). However, when species were moved north of their current range, added heat was neutral for recruitment (Fig. 1; Appendices E and F). These results are consistent with expectations (and recent observations) that it may be necessary for species to shift their ranges poleward to remain viable (Thomas et al. 2004, Doak and Morris 2010). Surprisingly, we found this result even when species were near their current northern range limit, where one might expect that increased temperatures would be beneficial. This suggests that species’ geographic ranges may already be limited by dispersal, as has been shown in many systems (Turnbull et al. 2000). In general, precipitation effects on recruitment were minimal (Appendices E and F), suggesting that the drying effect and earlier onset of drought conditions due to increased temperature may be more important for mediterranean prairie species than additional precipitation during the establishment phase (Appendix B). However, in 2011, the PNW experienced La Niña conditions with a prolonged spring rainy season, resulting in less moisture limitation during the growing season. Additional precipitation may have greater effects in drier years. Moreover, many of the species extend further south into more extreme mediterranean drought conditions, where changes in precipitation regimes may be more important (Crimmins et al. 2011).

Germination was the most significant hurdle for successful recruitment. Germination rates ranged from 1% to 15% (depending on species), with 85% of germinating plants surviving to year’s end (germination vs. recruitment $r^2 = 0.94$, $P < 0.001$ across all species). Added heat negatively impacted germination for species within their current range ($P \leq 0.012$) and became neutral as they moved outside this range (Appendix E). This finding is consistent with theory that posits longer lived plants (e.g., perennials vs. annuals) may be more buffered to climatic changes (Morris et al. 2008), as successful germination each year is not required for survival. Survivorship (from seedling to year’s end) also depended on a species’ current range, with more plants surviving when they were at their current northern range limit in the INL and HNL range groups (range group by site interaction, $P < 0.001$; Appendices E and G). However, unlike germination, warming decreased survivorship $\sim 20\%$, regardless of species’ current ranges ($P < 0.001$). This negative effect may be attributable to increased competition in the heated plots (as measured by aboveground net primary productivity [ANPP]; Appendix A). In support of this explanation, ANPP and survivorship were negatively correlated for half of the species tested (Appendix C).

In contrast to recruitment, plant size and seed production were not controlled by a species’ current range (range group by treatment interactions, $P \geq 0.34$).
Instead site and treatment effects were paramount. Surviving plants produced more biomass in heated ($P = 0.003$) and precipitation plots ($P = 0.022$), and these treatment effects were independent of one another (Appendix H). Seed production (measured for annuals only) was highly correlated with biomass (Pearson correlations, $0.64 < r < 0.98$), and results were similar to those for biomass. Nutrient availability was also greater in the heated treatments (Appendix A), suggesting that this size response is mediated by an indirect positive effect of heating on nutrients. Consistent with this proposed mechanism, both plant size and nutrient availability progressively decreased from south to north ($P < 0.001$; Appendix H). Indeed, size of most species was positively correlated with nitrogen and phosphorus availability (Appendix C). A greenhouse experiment with soils from all sites and four plant species verified these soil effects on plant growth were independent of climate (Wilson 2012). So although a species’ current range was an important determinant of whether a plant could establish, subsequent fitness effects appeared to be controlled by resource availability. In turn, resource availability was controlled by local soil type and temperature, but these two effects were independent of one another.

For the annual species, the net effect of recruitment and reproduction, $R_0$ (net reproductive rate), varied by species, site, and heating treatment (species $\times$ site $\times$ heat interaction, $P = 0.002$; Fig. 2). In general, across all species, $R_0$ was $\leq 1$, projecting population decline. However, $R_0$ tended to be higher for species when they were planted within their current range than beyond this range, though there were some exceptions (Fig. 2). The effect of heating on $R_0$ was more idiosyncratic among species. When heating affected $R_0$ it always had a negative effect. However, in every case except one (Thysanocarpus radians at the central site), this negative effect was only found within a species’ current range. Added precipitation never significantly affected $R_0$ (data not shown).

If these results are borne out over multiple years, they suggest that future climate change will decrease the ability of prairie species to persist in their current range because a negative effect of increased temperature on recruitment generally outweighed its positive effect on growth and seed production (Fig. 3). More years of data are needed to verify this finding for the annual species and to allow the perennial species to mature. This negative effect of warming was observed even at the coolest edge of species’ current ranges. However, when species were moved beyond their current range, the net effect of warming was neutral. This change occurred because the negative effect of warming on recruitment disappeared when species were moved outside their current range. The positive effect of warming on growth and seed production remained, but by itself was insufficient to drive a positive net effect. Importantly, vital rates did not respond consistently in their direction.

**Fig. 1.** Mean ± SE recruitment (defined as the probability of germinating and surviving to the end of year one) at each experimental site in heated and unheated plots in the Pacific Northwest, USA. Each panel shows a “range group” of four prairie plant species defined by the ecoregion of their northern range limit: (a) Lowest Northern Limit (41°–43° N), (b) Intermediate Northern Limit (43°–46° N), and (c) Highest Northern Limit (46°–50° N); N, northern site; C, central site; and S, southern site. Shaded bars indicate species that were planted within their current range and correspond to shaded ecoregions of inlaid maps. Unshaded bars indicate species that were moved north of their current range. Hatching in bars indicates temperature treatments $3^\circ C$ higher than ambient. Statistical tests were performed on z-score transformed data, but raw data are presented for clarity. ***$P < 0.001$ (significant heating effects within a site).
(e.g., survivorship vs. fitness) and magnitude to climate and current range limits (cf. Doak and Morris 2010). While local resource availability was an important control over some vital rates, the effects of heating and current range limits were remarkably consistent across sites and species, and were not obscured by idiosyncratic local site–species interactions. Despite our finding that it appears tractable to experimentally determine climate effects on various vital rates, most species distribution models do not incorporate demographic mechanisms (Buckley et al. 2010, Clark et al. 2011, McMahon et al. 2011, but see Midgley et al. 2010).

The extent to which species will be able to track changes in climate will depend on their ability to adapt to new conditions or to disperse, establish, and persist in new favorable habitats (Fig. 3). While we only addressed establishment and persistence, unprecedented rates of climate change may outpace species’ abilities to adapt, migrate, and disperse (Turnbull et al. 2000, Gaston 2009), particularly in today’s highly fragmented landscapes. Actions that increase habitat connectivity could facilitate natural migration to more suitable climatic conditions, while active prairie management that promotes genetic diversity could help maintain prairie species in current locations. Where these actions are insufficient or infeasible, assisted migration (managed relocation) may be necessary to prevent species’ extinctions (Vitt et al. 2010). Our short-term experimental results suggest that under future climate conditions there may be a need for such range shifts and that suitable habitats may be found poleward for a diverse suite of prairie plant species. However, there is a pressing need for longer-term experimental demographic studies and regional studies of long-range dispersal.

Fig. 2. Net reproductive rate, \( R_0 \) (mean ± SE; note log scale axis), at each site in heated (hatched bars) and unheated plots for the annual species (range group assignments are also indicated: LNL, Lowest Northern Latitude; INL, Intermediate Northern Latitude; and HNL, Highest Northern Latitude). Shaded bars indicate species that were planted within their current range. Different lowercase letters indicate significant differences \( (P < 0.05) \) among sites within a species. Asterisks indicate significant heating \( (H) \) effects within a site. Cases where bars are absent indicate an \( R_0 \) equal to zero.

\* P < 0.05; \** P < 0.01; \*** P < 0.001.
FIG. 3. General demographic responses of prairie plant species inside (shaded) and poleward beyond their current ranges to climate ($H$, heat increase of 3°C; $P$, precipitation increase of 20%) and local controls (gray arrows). Recruitment effects were driven by establishment, with negative heating effects inside species’ current ranges and no effects beyond (see Fig. 1; Appendices E and F). Fitness effects did not depend on current ranges, but instead responded positively to increased heat and precipitation (Appendices E and H). The net effect, $R_0$, of these nonuniform (and sometimes opposing) demographic parameters resulted in mixed responses for the six annual species (Fig. 2). A downward-pointing arrow (↓) indicates a negative response, an upward-pointing arrow (↑) indicates a positive response, and ns indicates no significant change. In cases of mixed responses, multiple symbols are ordered with the most common response first. Demographic responses include establishment (germination), survivorship (seedling to end of year one), recruitment (the product of establishment and survivorship; indicated by the dashed rectangle), fitness (growth for six perennials and growth and seed set for six annuals), and the net reproductive rate, $R_0$ (product of seed set and recruitment for the six annuals only; indicated by the solid rectangle). Also included are correlations among local factors (competition [NPP, net primary productivity] and nutrient availability; gray arrows) and specific demographic responses, indicated by (+) and (—) signs (Appendix C).

ACKNOWLEDGMENTS

We thank The Nature Conservancy (TNC), Center for Natural Lands Management (CNLM), and The Deer Creek Center for site use; TNC, CNLM, the City of Eugene, U.S. Bureau of Land Management, and Joint Base Lewis-McChord (U.S. Army) for native seed donations; Timothy Tomaszewski, Cody Evers, Hannah Wilson, Dani Fagan, Aarya Ferguson, Sean McKenzie, Belle Tegner, and numerous undergraduate volunteers for assistance with laboratory and field work; Ed Alverson for compiled lists of PNW prairie species and fidelity class; and Bruce Kimball for assistance with the heating technology. This research was funded by the Office of Science (Biological and Environmental Research; BER), U.S. Department of Energy, grant number DE-FG02-09ER604719, and publication costs were provided by the University of Oregon Library. The views and opinions of authors expressed herein do not necessarily state or reflect those of the U.S. Government or any agency thereof.

LITERATURE CITED


Wilson, H. E. 2012. Climate change effects on arbuscular mycorrhizal fungi and prairie plants along a Mediterranean climate gradient. Thesis. University of Oregon, Eugene, Oregon, USA.

SUPPLEMENTAL MATERIAL

Appendix A
Table of locations, climate data, and soils descriptions for experimental study sites (Ecological Archives E094-198-A1).

Appendix B
Figure of soil temperature and matric potential in the four climate treatments at each site (Ecological Archives E094-198-A2).

Appendix C
Table of selected species for the experiment (Ecological Archives E094-198-A3).

Appendix D
Supplemental methods on species selection (Ecological Archives E094-198-A4).

Appendix E
Table of ANOVA results (Ecological Archives E094-198-A5).

Appendix F
Figure of recruitment of individual species in the four climate treatments at each site (Ecological Archives E094-198-A6).

Appendix G
Figure of survivorship of each range group at each site (Ecological Archives E094-198-A7).

Appendix H
Figure of mean plant size in climate treatments and each study site across all range groups (Ecological Archives E094-198-A8).