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Abstract. Predicting the future of any given species represents an unprecedented challenge in light of the many environmental and biological factors that affect organismal performance and that also interact with drivers of global change. In a three-year experiment set in the Mongolian steppe, we examined the response of the common grass *Festuca lenensis* to manipulated temperature and water while controlling for topographic variation, plant–plant interactions, and ecotypic differentiation. Plant survival and growth responses to a warmer, drier climate varied within the landscape. Response to simulated increased precipitation occurred only in the absence of neighbors, demonstrating that plant–plant interactions can supersede the effects of climate change. *F. lenensis* also showed evidence of local adaptation in populations that were only 300 m apart. Individuals from the steep and dry upper slope showed a higher stress/drought tolerance, whereas those from the more productive lower slope showed a higher biomass production and a greater ability to cope with competition. Moreover, the response of this species to increased precipitation was ecotype specific, with water addition benefiting only the least stress-tolerant ecotype from the lower slope origin. This multifaceted approach illustrates the importance of placing climate change experiments within a realistic ecological and evolutionary framework. Existing sources of variation impacting plant performance may buffer or obscure climate change effects.

Key words: competition; *Festuca lenensis*; local adaptation; Northern Mongolia; open-top chamber (OTC); steppe grassland; stress; warming; watering.

INTRODUCTION

The Dark Side clouds everything. Impossible to see, the future is.

—Yoda (2002, *Star Wars* episode II)

Patterns of species abundance and distribution emerge from a complex interplay of ecological and evolutionary processes that involve interactions between abiotic and biotic factors. Therefore, understanding the impact of global change on biological systems requires a concerted multi-scalar and multidisciplinary effort (Williams et al. 2008) that integrates the sub-disciplines of community ecology, landscape ecology, and evolutionary ecology. An integrated approach that explores the interaction of global change factors with pre-existing sources of abiotic and biotic variation, including ecotypic differentiation, is necessary to understand the fates of species (Williams et al. 2008, Lavergne et al. 2010).

Future climate modifications are likely to affect community composition and structure not only directly

through abiotic changes, but also indirectly by modifying the direction and intensity of species interactions, including competition (Davis et al. 1998, Pearson and Dawson 2003, Levine et al. 2010), facilitation (Brooker 2006), mutualism, herbivory, or predation (Gilman et al. 2010). The outcome of climate modification through both direct and indirect effects is likely to vary along environmental gradients (Harte and Shaw 1995, Klein et al. 2004, Liancourt et al. 2012a, b). Understanding indirect effects of climate modification may be particularly important for plant communities where the direction and intensity of plant–plant interactions vary along environmental gradients (Grime 1974, Michalet et al. 2006). Based on the “stress gradient hypothesis,” competition is thought to rule at the benign end of stress gradients, while facilitation may occur when approaching the harsher end of a gradient, where it eventually wanes (Michalet et al. 2006). Although much attention has been paid to the net effects of climate change on plant communities, very few field-based experimental studies have explicitly included a test for the role of plant–plant interactions in this context (see Klanderud and Totland 2005, Adler et al. 2009, Rixen and Mulder 2009, Levine et al. 2010).

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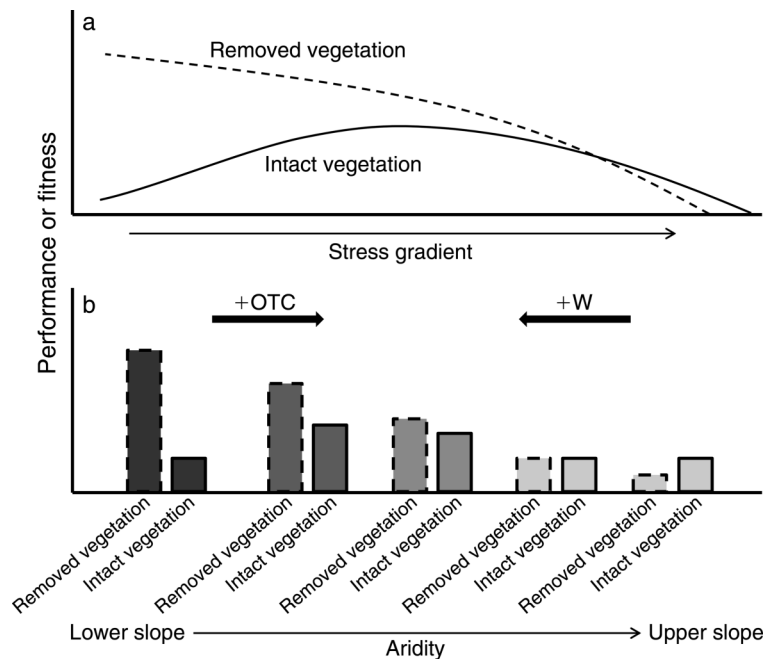


FIG. 1. Schematic representation of (a) the stress gradient hypothesis, where the dashed line represents the performance of a species without neighboring vegetation (removed vegetation) and the solid line represents its performance with neighboring vegetation (intact vegetation; analogous to the “physiological response curve” and “ecological response curve,” respectively, sensu Ellenberg 1953, 1954). The intensity and direction of plant–plant interactions (negative or positive) are obtained by comparing the two curves. The shift from competition to facilitation is expected to occur at the high-stress end of the gradient. The direct effect of climate change impacts physiological plant response (dashed line), whereas the net effect impacts the solid line. (b) Specific predictions for the direct effect and net effect of our climate manipulation on the upper and lower slope in the Mongolian steppe, corresponding to the two extremes of an aridity gradient produced by the slope. Arrows represent the expected effect of our climate manipulation, where the open-top chambers (+OTCs) are hypothesized to mainly increase water stress, and the Water treatment (+W) alleviates water stress. The dashed and solid lines correspond to the dashed and solid lines in panel (a). Each pair of bars is positioned along an aridity gradient from the lower to the upper slope, with dark gray representing less water stress and lighter gray indicating higher water stress.

The presence of ecotypic variation within species also presents a notable challenge for forecasting the effect of climate change. Local adaptation plays a prominent role in ecological and evolutionary processes (see Leimu and Fischer 2008) and is not rare (Hereford 2009). Ecotypic differentiation occurs even over short distances, such as along topographic or elevational gradients (e.g., McGraw and Antonovics 1983, Byars et al. 2007, Liancourt and Tielbörger 2009). Ecotypically differentiated populations perceive and respond differently to environmental conditions, and they may be differentially vulnerable to environmental change (Harte et al. 2004, Beierkuhnlein et al. 2011). The degree to which ecotypic variation determines a species’ response to either direct or indirect effects of climate change is still largely unknown (see Pearson and Dawson 2003, Harte et al. 2004, Lavergne et al. 2010).

We conducted an experiment in the steppe of northern Mongolia to investigate the interplay between abiotic factors and biotic interactions and the potential role of ecotypic variation in a species’ response to climate change across the landscape. Mongolian mountain steppe is limited both by temperature and water (see Liancourt et al. 2012a and references therein). Northern

Mongolia is predicted to experience above average rates of temperature increase, but, while precipitation is predicted to change over the coming century, there is no consensus on how (IPCC 2007, but see Sato et al. 2007). Our experiments included climate manipulation through open-top chambers (OTCs) and water addition, local topographic variation (drier steep, upper slope vs. more productive, gentle lower slope), and presence or absence of plant–plant interactions (vegetation present or removed). We included within these experimental factors reciprocal transplantation of a common species from the same two topographic origins to test for (1) local adaptation to abiotic and biotic conditions and (2) the response of these putative ecotypes to direct and indirect effects of our climate manipulation in both topographic locations.

Our predictions for the effects of climate manipulations and their effect on plant–plant interactions follow the “stress gradient hypothesis” (Fig. 1; Grime 1973, Michalet et al. 2006), predicting that OTCs should accentuate stress and decrease competition intensity where water is more limiting (Elmendorf et al. 2012, Liancourt et al. 2012a, b). Water addition should alleviate stress and increase competition intensity (Fig.

1). If local adaptation occurs in our system, we predict that (1) individuals from the drier, upper slope should be more stress tolerant and those from the more productive, lower slope should be more competitive. It follows that (2) water addition could affect individuals from the upper slope negatively, owing to the subsequent increase in competition with neighbors, while a deterioration of environmental conditions could even affect them positively because of decreased competition intensity. Finally, vice versa, (3) the individuals from the lower slope should be more vulnerable to deterioration of environmental conditions, but receive benefits from their improvement.

METHODS

Study site and target species

For this study, experimental treatments were applied from early June to mid-August in 2009, 2010, and 2011 on a south-facing slope in the Dalbay river valley (51°01.405' N, 100° 45.600' E; 1670 to 1800 m above sea level [a.s.l.]; see Plate 1). Regionally, the average annual air temperature is -4.5°C , with average monthly temperatures from -21°C (January) to 12°C (July). Average annual precipitation over the last 40 years was 265 mm. An on-site meteorological station recorded summer rainfall (June to August) of 201 mm (2009), 178 mm (2010), and 137 mm (2011). There was no snow cover when the experiment was set up any year, but new growth was not present for most plant species. The bedrock is of Cenozoic volcanic deposits, and the soil is sandy loam, of alluvial origin, and classified as a non-carbonated Dark Kastanozem (Aridic Boroll or Typic Ustolls).

We worked at two locations along a topographic, aridity gradient; the wetter lower slope where we expected plant competition to be more intense, and the drier upper slope, which is a more stressful environment. The lower slope location (~ 1670 m a.s.l.) is flat or has a gentle incline, and the upper slope location (~ 1800 m a.s.l.) has an incline of $\sim 20^{\circ}$; the distance between the two locations was ~ 300 m. The lower slope is characterized by greater total soil nitrogen and carbon, plant biomass, and litter (Casper et al. 2012). Soil moisture is likely to be the main driver of these differences observed between the upper, steep and the lower, gentle slope (Casper et al. 2012, Liancourt et al. 2012a), with a seasonal average for the volumetric soil moisture of the surface soil being $\sim 40\%$ drier on the upper slope than on the lower (Liancourt et al. 2012a). The average seasonal daytime air temperatures (June–August, 06:00–21:00 hours) measured on-site over the course of the experiment did not differ between the two slope locations ($\sim 15^{\circ}\text{C}$), whereas nighttime air temperatures were colder for the lower slope, likely as a consequence of cold-air drainage into the river valleys (8.4°C at the upper slope vs. 5.3°C at the lower slope). In 2009, vascular plant cover of the lower and upper slope was 78% and 64%, respectively (Partnerships for Inter-

national Research and Education [PIRE] Mongolia, unpublished data).

Typical for mountain steppe, the vegetation is a mixture of sedges, grasses, and short forbs, but the species composition differs between the two slope locations. The lower slope is dominated by *Carex pediformis* and *Potentilla acaulis*. The latter is the most abundant species on the upper slope (See Liancourt et al. 2012b for a complete list and relative abundance). We selected *Festuca lenensis* Drobow (Poaceae), a short C_3 bunchgrass (10–15 cm high), as the target species in our experiment due to its abundance ($\sim 10\%$ cover) at both slope locations. *F. lenensis* is a characteristic/dominant species of mountain steppe in northern Mongolia (Fernandez-Gimenez and Allen-Diaz 2001). Precise information about the ecology of the species is sparse. It is of central Asia–south Siberian origin and forms a large circumpolar range in the Holarctic (Yurtsev 2001). Its morphological similarity with *Festuca ovina* suggests a “stress-tolerant” strategy (sensu Grime 1974), and it has been described as drought and cold tolerant, i.e., cryo and xerophytic (e.g., Namzalov et al. 2012).

Experimental design

We manipulated climate at the two slope locations using open-top passive warming chambers (OTCs), a common design used in climate-warming studies (see Elmendorf et al. 2012 for recent review), especially in remote sites such as ours where there is no electricity. The hexagonal OTCs were 1.0 m wide at the top and 1.5 m at the bottom, 40 cm tall, and made of Sun-Lite HP fiberglass glazing mounted on a clear Lexan frame (Solar Components, Manchester, New Hampshire, USA). One OTC and one control (untreated plot of the same dimensions) were spatially grouped within a 9×9 m block; there were eight replicate blocks on the lower slope and seven blocks on the upper slope. On the drier upper slope only, one additional OTC and control plot per block received supplemental water weekly using river water, for 11 consecutive weeks from June to August. Each water application simulated a 4.5-mm rainfall, resulting in roughly 20% more water for the growing season (Water treatment). All blocks were fenced to exclude livestock.

OTCs alter both air temperature and soil moisture. At our site, air temperatures within OTCs were elevated by 1.5°C in the day and depressed by -0.2°C at night on average (Liancourt et al. 2012b). On the lower slope, OTCs also decrease volumetric soil moisture by an average of 35% and by 30% in the unwatered plots on the upper slope. More detailed description of the experimental treatments' effect on volumetric soil moisture and temperature in 2009 and 2010 is reported in Liancourt et al. (2012a, b).

In order to quantify the intensity and the direction (negative or positive) of plant–plant interactions within our experiment, we compared the survival and growth of

F. lenensis with and without neighbors (Vegetation treatment). Within each hexagonal experimental plot, two individuals were planted in one corner where the vegetation was removed and two others were planted in the corner directly opposite where the vegetation was left intact. Corners consisted of 0.55-m² triangular areas, formed by three adjacent vertices of the hexagon (Fig. 2). The hexagonal plots were always oriented such that two parallel sides faced north–south. Vegetation was removed from the eastern corner in half of the plots and the western corner in the other half. We used a long serrated knife to cut away aboveground plant material, including litter, and to trench around the perimeter of the triangular area to exclude roots from surrounding vegetation. We kept these areas vegetation free by weekly weeding and continued trenching.

The two *F. lenensis* individuals planted into a corner (either vegetated or unvegetated) originated from different slope locations: one from the upper slope and the other from the lower slope (Fig. 2). This design enabled us to look for evidence of ecotypic differentiation (based on Origin), including any difference in their response to climate manipulation or to the presence/absence of vegetation. Because the experiment was repeated at each slope location, we were able to assess whether individuals planted in their native slope location performed better than individuals originating from the alternate slope location.

Candidate individuals for planting into the experimental plots came from 60 distinct clumps of *F. lenensis* collected on the upper slope and 60 collected on the lower slope in mid-June 2009. Each clump included several tillers, including roots, and each clump was kept in a separate cup of water to stimulate new root production before transplantation two weeks later. For planting, each individual consisted of 3–4 tillers (9–12 leaves) originating from a single clump, chosen randomly from among the 60 clumps collected from the appropriate slope location. No clump was represented more than once among the plantings on either slope. Individuals were transplanted with naked roots to limit soil import and watered daily for two weeks to reduce transplant shock. Individuals dying within three weeks were replaced with another from the same clump. All transplants were alive at the end of the summer 2009, and subsequent mortality was considered part of the experiment. Survival and total aboveground biomass (vegetative plus reproductive) were quantified at the end of the experiment. Individuals were harvested on 29 and 30 July 2011, air dried for a week, and weighed.

Measurements of abiotic variables

To help interpret plant responses to our experimental treatments, we measured plant available nitrogen and photosynthetic active radiation (PAR) in 2010 in all of our experimental treatments. Available NO₃[−] and NH₄⁺ were measured using plant root simulator (PRS) probes (Western Ag Innovations, Saskatoon, Saskatchewan,

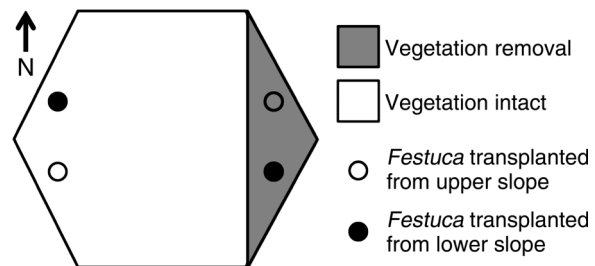


FIG. 2. Illustration of a plot, showing the Vegetation treatment and the transplanted individuals of *Festuca lenensis* from the lower and upper slope (Origin).

Canada; more information *available online*),⁶ which employ ion-exchange membranes. In late June, two anion and two cation probes were inserted into each unvegetated and vegetated corner where *F. lenensis* had been planted and left in place for 21 days (Casper et al. 2012). Available NO₃[−] and NH₄⁺ were summed and expressed in micrograms per 10 square centimeter of ion-exchange surface. In 2010, to explore how neighboring vegetation impacted light levels, PAR measurements were made horizontal to the soil, at the ground surface, between 11:00 and 12:00 hours (solar noon) on a cloudless day at the peak of the growing season (mid-July) using a light sensor (LI-1400; LI-COR, Lincoln, Nebraska, USA). PAR measurements were made in all plots, and depending on the treatment, sensors were placed either under the vegetation or next to target *F. lenensis* individual in the unvegetated areas.

Statistical analyses

Statistical analyses examining the effect of experimental treatments on plant performance, total available N, and PAR were conducted separately for the upper and lower slope locations due to the presence of the Water treatment on the upper slope location but not the lower (i.e., no full factorial design). For the lower slope, the ANOVA model used to examine aboveground biomass included Chamber treatment, Vegetation treatment, and Origin of *F. lenensis* as fixed effects, and Block and the interaction between Block and the aforementioned factors as random effects. For the upper slope analysis, the Water treatment was included as an additional fixed effect. For both the lower and upper slope analyses, the highest order interaction containing the Block effect served as the residual error because the experiments were randomized block designs.

Survival of plants under different experimental treatments was examined using logistic regression. The effect of Block was not included because random effects cannot be handled with standard methods of logistic regression. Ignoring random effects in logistic regressions tends to make tests of significance more conservative. Models did not converge when the three-way and

⁶ <http://www.westernag.ca/innov/prs-probes/>

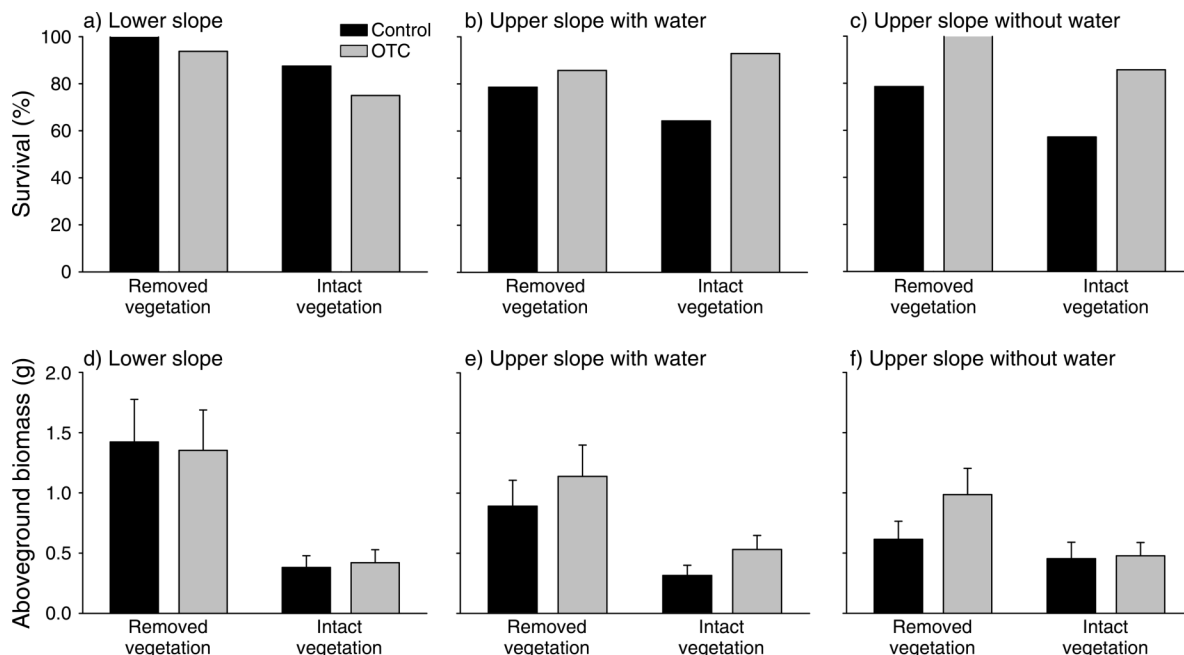


FIG. 3. Survival and aboveground biomass (mean + 95% CI) of *Festuca lenensis* as affected by OTC and neighboring vegetation on (a, d) the lower slope, (b, e) the upper slope with water, and (c, f) on the upper slope without water. The data presented are pooled across Origin and illustrate the significant effect of Vegetation on the lower slope and the significant Chamber effect (OTC) on the upper slope for survival, and the significant effect of Vegetation on the lower slope and the significant Chamber effect and Vegetation \times Water interaction on the upper slope for aboveground biomass. See Table 1 for statistical results.

four-way interaction terms were included, and these were removed to improve the fit and the stability of the parameter estimates.

Total available N and PAR were also examined using ANOVA; in response to Chamber treatment and Vegetation treatment for the lower slope and in response to Chamber, Vegetation, and Water treatment for the upper slope. Aboveground biomass and total available N data were ln-transformed prior to analysis. Analyses were carried out with JMP 8.0 (SAS Institute 2008).

RESULTS

Stress gradient

Variation in target plant performance was consistent with our two slope locations representing different points along opposing gradients of abiotic stress and competition from neighbors. Pooled across Origin, target individuals in control plots without vegetation produced 2.3 times greater biomass on the lower slope than on the upper slope (t test $P < 0.001$; Fig. 3), consistent with the lower slope being the more productive, less stressful environment. Target individual survival was also higher on the lower slope (lower vs. upper slope, 94% vs. 68% survival, respectively; χ^2 test $P < 0.01$; Fig. 3); this lower slope vs. upper slope comparison was made for individuals in control, unwatered plots only, pooling across both Origin and Vegetation treatments. Although the presence of neighbors reduced plant biomass at both slope locations

(Table 1, Fig. 3), the magnitude of the effect (and thus the strength of competition) was greater on the lower slope (Fig. 3). Greater competition on the lower slope was also expressed as decreased survival in the presence of vegetation, while the presence of vegetation did not affect survival significantly on the upper slope (Table 1, Fig. 3).

Climate manipulation

The effect of OTCs on plant performance was not consistent across the two slope locations. There was no effect of OTCs on the lower slope (Fig. 3a, d), but on the upper slope, OTCs increased both survival and biomass (Table 1, Fig. 3b, c, e, f).

The Water treatment was applied on the upper slope only and did not have consistent effects across the other experimental factors. Watering increased target plant biomass in the unvegetated treatment, but not the vegetated treatment (Vegetation \times Water interaction; Table 1, Fig. 3e, f). Survival was higher in the watered treatment for individuals of *F. lenensis* originally collected on the lower slope, but survival was higher in the unwatered treatment for individuals originating on the upper slope (Origin \times Water interaction; Table 1, Fig. 4a).

Plant origin

Two lines of evidence suggest functional differences for *F. lenensis* originating from the two slope locations;

TABLE 1. *P* values for the mixed-model ANOVAs for light availability, total available soil nitrogen, and aboveground biomass of the target species and for the logistic regression for survival.

Effects	Lower slope				Upper slope			
	Light	Available N	Biomass	Survival	Light	Available N	Biomass	Survival
Vegetation	0.004	0.004	<0.001	0.0131	0.012	0.022	<0.001	ns
Chamber	0.015	0.048	ns	ns	ns	ns	0.0036	0.0034
Water	ns	ns	ns	ns
Origin	0.045	ns	ns	ns
V × C	ns	...	ns	ns	ns	ns	ns	ns
V × W	ns	ns	0.0238	ns
C × W	ns	ns	ns	ns
O × V	0.0072	ns	ns	ns
O × C	ns	ns	ns	ns
O × W	ns	0.0353

Notes: Only significant results are reported ($P < 0.05$); ns indicates nonsignificant effects. Three- and four-way interactions were not included in the logistic regression used to analyze survival, and were not significant for the mixed-model ANOVAs and are not shown in the table. Abbreviations are: V, Vegetation; C, Chamber; W, Water; and O, Origin. Ellipses indicate that the effect did not apply for the variable or the location.

in general, plants performed better in their home environment. (1) One piece of evidence comes from the Origin × Water interaction described in the previous section. On the upper slope, plants originating from the upper slope showed higher survival without water than did those originating on the lower slope, and water addition increased survival of plants of lower slope origin but decreased survival for plants of upper slope origin (Table 1, Fig. 4a). (2) On the lower slope, plants originating there grew larger overall (Origin main effect; Table 1, Fig. 4b) and were slightly but significantly less affected by the presence of vegetation than were plants originating on the upper slope (Vegetation × Origin interaction; Table 1, Fig. 4b).

Abiotic variables

Plant available nitrogen and PAR each responded to the same experimental treatments. Vegetation reduced nitrogen (Table 1, Fig. 5) and PAR on both the upper and lower slope, where the effect size was greater. For PAR, vegetation intercepted 21% and 45% on the upper and lower slope, respectively. Chambers increased nitrogen (see Fig. 5) and also decreased PAR by 16% on the lower slope only (Table 1). The effects of Vegetation and Chambers were additive, not interacting with each other or with the Water treatment to affect either nitrogen or PAR.

DISCUSSION

Our experiment clarifies how predicted changes in climate will interact with existing landscape-scale variation in abiotic and biotic factors to affect plant performance in the Mongolian steppe. We show that (1) differential effects of climate manipulation occur at two topographic locations, which also differ naturally in plant productivity and abiotic stress, (2) that strong plant–plant competition may supersede direct effects of changing precipitation on plant performance, and (3) evidence consistent with ecotypic variation within our target species, expressed as plants from each slope

location having greater performance in their home location and differential responses to neighbors and to supplemental watering.

The first source of variation we examined was related to different abiotic and biotic contexts associated with the two slope locations. We demonstrated a difference in

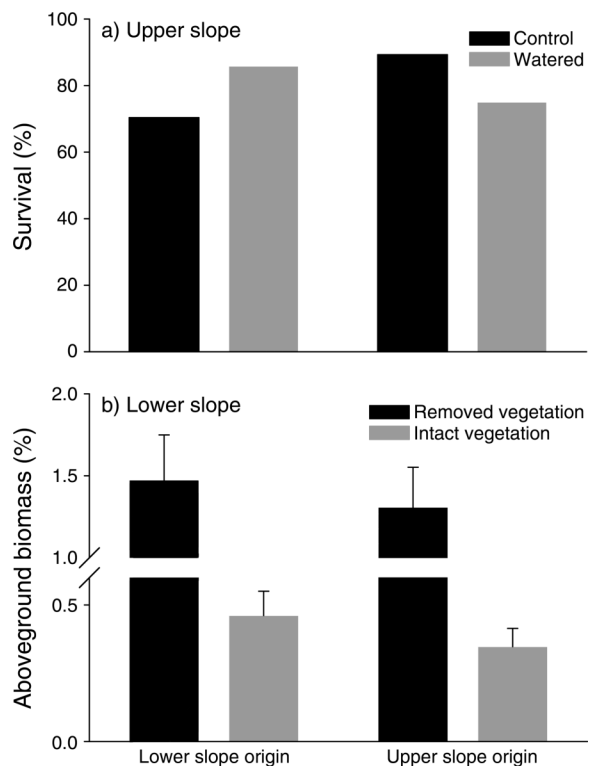


FIG. 4. (a) Significant Water × Origin interaction on the survival of *Festuca lenensis* on the upper slope where data presented are pooled across Chamber and Vegetation treatments, and (b) Significant Origin × Vegetation interaction on aboveground biomass of *Festuca lenensis* (mean + 95% CI) on the lower slope where data presented are pooled across Chamber treatment. See Table 1 for statistical results.

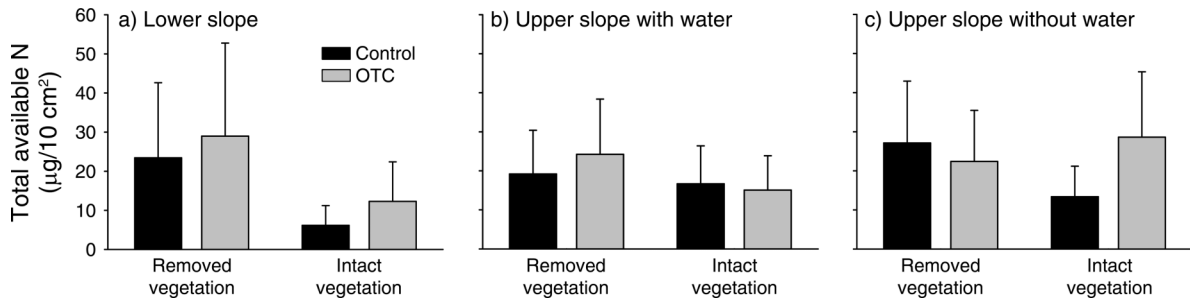


FIG. 5. Total available soil nitrogen as affected by OTC and neighboring vegetation on (a) the lower slope, (b) the upper slope with water, and (c) on the upper slope without water, illustrating the significant Vegetation and Chamber effect on the lower slope and the Vegetation effect on the upper slope.

competition intensity, i.e., how much neighboring vegetation reduces plant performance, between the two slope locations with results supporting the notion of a trade-off between competition intensity and stress (Grime 1974). Exactly how the intensity and direction of plant–plant interactions vary along environmental gradients has been the topic of fierce debates over the last three decades (e.g., Mahmoud and Grime 1976, Tilman and Wedin 1991, Reader et al. 1994, Rajaniemi 2002, Michalet et al. 2006), but in our system, greater productivity and competition intensity on the lower slope is easily explained by its greater water availability (Liancourt et al. 2012a, see also Kadmon 1995, Corcket et al. 2003, Liancourt et al. 2005a, Liancourt and Tielbörger 2009).

That water availability influences plant–plant competition is supported by the increase in competition intensity on the upper slope caused by the supplemental watering treatment. Additionally, the greater competition intensity measured on the lower slope relative to the upper slope is consistent with our findings that vegetation also causes a greater reduction in light and N availability on the lower slope. The environmental differences between the more productive lower slope and the drier upper slope may not have been great enough to see, from the target plant's perspective, the shift from competition to facilitation as predicted by the “stress gradient hypothesis” (Fig. 1; Choler et al. 2001, Liancourt et al. 2005a, Michalet et al. 2006). Alternatively, neighboring vegetation may not be capable of ameliorating water limitation at the harsh end of the gradient (Gross et al. 2010).

We expected OTCs to increase stress (Elmendorf et al. 2012), especially on the upper slope, since they are known to increase temperature and they decreased soil moisture by partially intercepting rainfall in our experiment (Liancourt et al. 2012a). Surprisingly, OTCs increased survival and growth of *F. lenensis* on the drier and warmer upper slope while having no effect on the lower. The positive OTC effect on only the upper slope is not likely to be due strictly to a reduction in cold stress since the upper slope is warmer than the lower at night and has similar temperatures during the day. We believe, instead,

that a decrease in evapotranspiration (Liancourt et al. 2012a), probably due to wind interception, might underlie the observed positive effect of OTCs (Marion et al. 1997). We have documented that the soil desiccation rate after a rainfall is slower inside OTCs than control plots (Liancourt et al. 2012a), which could reflect wind interception and, therefore, higher relative humidity inside the OTCs. On the upper slope more than the lower, the benefits of wind interception (see Whitehead 1962) and elevated temperature might offset the reduced soil moisture caused by OTCs. Unfortunately, our data set does not allow us to compare whether wind speed differs between the lower and upper slope.

It is also noteworthy that climate manipulation by OTCs did not change competition intensity at either slope location. Following our expectation that OTCs would create a more stressful environment, we expected competition intensity to decline in OTCs (Grime 1973), or even to observe a shift from competition to facilitation (Fig. 1; Michalet et al. 2006). However, the difference in plant performance between the vegetated and the unvegetated treatments was not modified by the OTCs, even on the upper slope where the overall effect of OTCs was positive. Likewise, OTCs did not interact with supplemental watering to affect plant performance, which would be expected if watering ameliorated the water stress imposed by the OTCs. Since the water addition did increase competition intensity (see also Kadmon 1995, Corcket et al. 2003, Liancourt et al. 2005b), we predict that future changes in the amount or temporal patterning of precipitation will have a greater effect than temperature changes on plant–plant competition with potentially large repercussions for the composition of this steppe community. However, it is important to realize that we used only a single target species in this experiment, and that responses to such treatments are often species specific (Grime 1973). Even though our target species was chosen for its local abundance, its importance as a characteristic species of mountain steppe, and its large distribution range, it may not be representative of other species in the system. Competition experienced by *F. lenensis* in this experiment was strong and, based on its survival, its growth in



PLATE 1. View of the south-facing slope of the Dalbay River Valley, northern Mongolia, where the climate manipulations were conducted. Open-top warming chambers (used in the present experiment) and rain-out shelters (for additional research) are visible on the lower and upper slopes. Photo credit: B. Boldgiv.

the absence of vegetation, and its morphology, its success in the system is likely to be due to its tolerance to stress or its ability to take advantage of local disturbance rather than its competitive ability. Therefore, it is possible that for a different target species with better competitive response ability and lesser stress tolerance ability, OTCs would create a more stressful environment, or an interaction could occur between warming and vegetation removal.

Another source of variation within the landscape that could influence a species' response to climate change is local plant adaptation (Harte et al. 2004). Our results are consistent with ecotypic variation within our target species over a distance of 300 m. Although the performance differences we observed were small (Hereford 2009), plants of each origin performed better in their home environment, which is consistent with local adaptation (Kawecki and Ebert 2004). On the lower slope, local individuals grew to a larger body size and, to a smaller extent, showed a stronger ability of the plants to cope with the negative effect of neighbors (i.e., stronger competitive response *sensu* Goldberg and Landa 1991). Individuals from the upper slope exhibited greater survival in their home location without supplemental water, suggesting their greater stress tolerance. A trade-off between stress tolerance and competitive response ability has been described previously when comparing different species (e.g., Suding et al. 2003, Liancourt et al. 2005a), but our results provide evidence for its occurrence *within* a species (e.g., Liancourt and Tielbörger 2009).

Experiments coupling the removal of vegetation with traditional reciprocal transplantation to study local adaptation are still uncommon (e.g., Knight and Miller 2004, Bischoff et al. 2006, Sambatti and Rice 2007, Rice and Knapp 2008, Liancourt and Tielbörger 2009, Ariza and Tielbörger 2011), and thus few field studies have demonstrated a potential role of competition in ecotypic differentiation (Knight and Miller 2004, Bischoff et al. 2006, Rice and Knapp 2008, Liancourt and Tielbörger 2009). Interestingly, the different strategies identified between the individuals from the lower and the upper slope did not translate into a differential response with respect to OTCs or to the increased competition generated by water addition. However, consistent with our hypothesis, only individuals from the lower slope, which we view as the least stress tolerant "ecotype," benefited from the water addition on the upper slope. Therefore, ecotypic variation is a relevant factor to consider when predicting the effect of global change.

While we invoke local adaptation to explain performance differences between plant origins, we recognize that such differential responses could also be due to environmental imprints on the source plant material or other maternal, including epigenetic, effects (Roach and Wulff 1987, Bossdorf et al. 2008). We did take great care to standardize the initial sizes of individuals, and we kept them under identical conditions for two weeks before planting. The lack of any indoor growth facilities precluded our culturing plants for long periods or working

with second-generation plants, which would have minimized residual environmental influences of plant origin.

Our evaluation of climate change consequences in the context of existing biotic and abiotic variation across the landscape allows us to make several generalizations. The sort of modification imposed by OTCs (increased temperature and decreased soil moisture and wind) will affect the upper slope more than the lower slope. Moreover, just a 20% increase in summer precipitation, manipulated as one additional application of 4.5 mm of rain per week, is enough to trigger a significant growth response for *F. lenensis* on the upper slope. However, because the benefit of one additional rainfall per week was only apparent for individuals growing without competition, it is clear that biotic interactions can supersede a particular species' response to climate change. Should the performance differences attributable to plant origin be genetic, climate change could have intriguing implications for this species' population structure. Precipitation increases would improve water availability on the upper slope, making it more hospitable to ecotypes from the lower slope than it is presently and potentially resulting in a redistribution of genotypes across the landscape.

In summary, we show that climate change will not produce consistent consequences across the landscape even for the same species and also that existing abiotic and biotic sources of variation in plant performance may buffer or even obscure climate change effects. The "stress gradient hypothesis" appears to offer a solid framework for evaluating the contingent effects of changes in a single resource such as water. Nevertheless, predicting plant responses to all concurrent climate change effects appears more challenging than expected.

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LITERATURE CITED

- Adler, P. B., J. Leiker, and J. M. Levine. 2009. Direct and indirect effects of climate change on a prairie plant community. *PLoS ONE* 4:e6887.
- Ariza, C., and K. Tielbörger. 2011. An evolutionary approach to studying the relative importance of plant-plant interactions along environmental gradients. *Functional Ecology* 25:932–942.
- Beierkuhnlein, C., D. Thiel, A. Jentsch, E. Willner, and J. Kreyling. 2011. Ecotypes of European grass species respond differently to warming and extreme drought. *Journal of Ecology* 99:703–713.
- Bischoff, A., et al. 2006. Detecting local adaptation in widespread grassland species: the importance of scale and local plant community. *Journal of Ecology* 94:1130–1142.
- Bosdorf, O., C. L. Richards, and M. Pigliucci. 2008. Epigenetics for ecologists. *Ecology Letters* 11:106–115.
- Brooker, R. W. 2006. Plant-plant interactions and environmental change. *New Phytologist* 171:271–284.
- Byars, S. G., W. Papst, and A. A. Hoffmann. 2007. Local adaptation and cogradient selection in the alpine plant, *Poa hiemata*, along a narrow altitudinal gradient. *Evolution* 61:2925–2941.
- Casper, B. B., R. Goldman, A. Lkhagva, B. R. Helliker, A. F. Plante, L. A. Spence, P. Liancourt, B. Boldgiv, and P. S. Petraitis. 2012. Legumes mitigate ecological consequences of a topographic gradient in a northern Mongolian steppe. *Oecologia* 169:85–94.
- Choler, P., R. Michalet, and R. M. Callaway. 2001. Facilitation and competition on gradients in alpine plant communities. *Ecology* 82:3295–3308.
- Corcket, E., P. Liancourt, R. M. Callaway, and R. Michalet. 2003. The relative importance of competition for two dominant grass species, as affected by environmental manipulations in the field. *Ecoscience* 10:186–194.
- Davis, A. J., L. S. Jenkinson, J. H. Lawton, B. Shorrocks, and S. Wood. 1998. Making mistakes when predicting shifts in species range in response to global warming. *Nature* 391:783–786.
- Ellenberg, H. 1953. Physiologisches und ökologisches Verhalten derselben Pflanzenarten. *Berichte der Deutschen botanischen Gesellschaft* 65:351–362.
- Ellenberg, H. 1954. Über einige Fortschritte der kausalen Vegetationskunde. *Vegetatio* 5/6:199–211.
- Elmendorf, S. C., et al. 2012. Global assessment of experimental climate warming on tundra vegetation: heterogeneity over space and time. *Ecology Letters* 15:164–175.
- Fernandez-Gimenez, M., and B. Allen-Diaz. 2001. Vegetation change along gradients from water sources in three grazed Mongolian ecosystems. *Plant Ecology* 157:101–118.
- Gilman, S. E., M. C. Urban, J. Tewksbury, G. W. Gilchrist, and R. D. Holt. 2010. A framework for community interactions under climate change. *Trends in Ecology and Evolution* 25:325–331.
- Goldberg, D. E., and K. Landa. 1991. Competitive effect and response: hierarchies and correlated traits in the early stages of competition. *Journal of Ecology* 79:1013–1030.
- Grime, J. P. 1973. Competitive exclusion in herbaceous vegetation. *Nature* 242:344–347.
- Grime, J. P. 1974. Vegetation classification by reference to strategies. *Nature* 250:26–31.
- Gross, N., P. Liancourt, P. Choler, K. N. Suding, and S. Lavorel. 2010. Strain and vegetation effects on limiting resources explain the outcomes of biotic interactions. *Perspectives in Plant Ecology, Evolution and Systematics* 12:9–19.
- Harte, J., A. Ostling, J. L. Green, and A. Kinzig. 2004. Biodiversity conservation: Climate change and extinction risk. *Nature* 430:33.
- Harte, J., and R. Shaw. 1995. Shifting dominance within a montane vegetation community: results of a climate-warming experiment. *Science* 267:876–880.
- Hereford, J. 2009. A quantitative survey of local adaptation and fitness trade-offs. *American Naturalist* 173:579–588.
- IPCC. 2007. Climate change 2007: the physical science basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. S. Solomon, D. Qin, M. Manning, Z. Chen, M. Marquis, K. B. Averyt, M. Tignor, and H. L. Miller, editors. Cambridge University Press, Cambridge, UK.
- Kadmon, R. 1995. Plant competition along soil moisture gradients: a field experiment with the desert annual *Stipa capensis*. *Journal of Ecology* 83:253–262.

- Kawecki, T. J., and D. Ebert. 2004. Conceptual issues in local adaptation. *Ecology Letters* 7:1225–1241.
- Klanderud, K., and Ø. Totland. 2005. The relative importance of neighbours and abiotic environmental conditions for population dynamic parameters of two alpine plant species. *Journal of Ecology* 93:493–501.
- Klein, J. A., J. Harte, and X. Zhao. 2004. Experimental warming causes large and rapid species loss, dampened by simulated grazing, on the Tibetan Plateau. *Ecology Letters* 7:1170–1179.
- Knight, T. M., and T. E. Miller. 2004. Local adaptation within a population of *Hydrocotyle bonariensis*. *Evolutionary Ecology Research* 6:103–114.
- 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.
- Leimu, R., and M. Fischer. 2008. A meta-analysis of local adaptation in plants. *PLoS ONE* 3:e4010.
- Levine, J. M., A. K. McEachern, and C. Cowan. 2010. Do competitors modulate rare plant response to precipitation change? *Ecology* 91:130–140.
- Liancourt, P., R. M. Callaway, and R. Michalet. 2005a. Stress tolerance and competitive-response ability determine the outcome of biotic interactions. *Ecology* 86:1611–1618.
- Liancourt, P., E. Corcket, and R. Michalet. 2005b. Stress tolerance abilities and competitive responses in a watering and fertilization field experiment. *Journal of Vegetation Science* 16:713–722.
- Liancourt, P., A. Sharkhuu, L. Ariuntsetseg, B. Boldgiv, B. R. Helliker, A. F. Plante, P. S. Petraitis, and B. B. Casper. 2012a. Temporal and spatial variation in how vegetation alters the soil moisture response to climate manipulation. *Plant and Soil* 351:249–261.
- Liancourt, P., L. A. Spence, B. Boldgiv, A. Lkhagva, B. Helliker, B. B. Casper, and P. S. Petraitis. 2012b. Vulnerability of the northern Mongolian steppe to climate change: insights from flower production and phenology. *Ecology* 93:815–824.
- Liancourt, P., and K. Tielbörger. 2009. Competition and a short growing season lead to ecotypic differentiation at the two extremes of the ecological range. *Functional Ecology* 23:397–404.
- Mahmoud, A., and J. P. Grime. 1976. An analysis of competitive ability in three perennial grasses. *New Phytologist* 77:431–435.
- Marion, G. M., G. H. Henry, D. W. Freckman, J. Johnstone, G. Jones, M. H. Jones, E. Lévesque, U. Molau, P. Mølgaard, A. N. Parsons, J. Svoboda, and R. A. Virginia. 1997. Open-top designs for manipulating field temperature in high-latitude ecosystems. *Global Change Biology* 3:20–32.
- McGraw, J. B., and J. Antonovics. 1983. Experimental ecology of *Dryas octopetala* ecotypes: i. Ecotypic differentiation and life-cycle stages of selection. *Journal of Ecology* 71:879–897.
- Michalet, R., R. W. Brooker, L. A. Cavieres, Z. Kikvidze, C. J. Lortie, F. I. Pugnaire, A. Valiente-Banuet, and R. M. Callaway. 2006. Do biotic interactions shape both sides of the humped-back model of species richness in plant communities? *Ecology Letters* 9:767–773.
- Namzalov, B., S. Kholboeva, A. Korolyuk, T. Baskhaeva, M. Tsirenova, and A. Mongush. 2012. Features of structure in zonal forest-steppe ecotone of South Siberia and Central Asia. *Arid Ecosystems* 2:78–85.
- Pearson, R. G., and T. P. 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.
- Rajaniemi, T. K. 2002. Why does fertilization reduce plant species diversity? Testing three competition-based hypotheses. *Journal of Ecology* 90:316–324.
- Reader, R. J., et al. 1994. Plant competition in relation to neighbor biomass: an intercontinental study with *Poa pratensis*. *Ecology* 75:1753–1760.
- Rice, K. J., and E. E. Knapp. 2008. Effects of competition and life history stage on the expression of local adaptation in two native bunchgrasses. *Restoration Ecology* 16:12–23.
- Rixen, C., and C. P. H. Mulder. 2009. Species removal and experimental warming in a subarctic tundra plant community. *Oecologia* 161:173–186.
- Roach, D. A., and R. D. Wulff. 1987. Maternal effects in plants. *Annual Review of Ecology and Systematics* 18:209–235.
- Sambatti, J. B. M., and K. J. Rice. 2007. Functional ecology of ecotypic differentiation in the Californian serpentine sunflower (*Helianthus exilis*). *New Phytologist* 175:107–119.
- SAS Institute. 2008. JMP version 8.0. SAS Institute, Cary, North Carolina, USA.
- Sato, T., F. Kimura, and A. Kitoh. 2007. Projection of global warming onto regional precipitation over Mongolia using a regional climate model. *Journal of Hydrology* 333:144–154.
- Suding, K. N., D. E. Goldberg, and K. M. Hartman. 2003. Relationships among species traits: separating levels of response and identifying linkages to abundance. *Ecology* 84:1–16.
- Tilman, D., and D. Wedin. 1991. Dynamics of nitrogen competition between successional grasses. *Ecology* 72:1038–1049.
- Whitehead, F. H. 1962. Experimental studies of the effect of wind on plant growth and anatomy. *New Phytologist* 61:59–62.
- Williams, S. E., L. P. Shoo, J. L. Isaac, A. A. Hoffmann, and G. Langham. 2008. Towards an integrated framework for assessing the vulnerability of species to climate change. *PLoS Biology* 6:e325.
- Yurtsev, B. A. 2001. The Pleistocene “tundra-steppe” and the productivity paradox: the landscape approach. *Quaternary Science Reviews* 20:165–174.