

Northward displacement of optimal climate conditions for ecotypes of *Eriophorum vaginatum* L. across a latitudinal gradient in Alaska

JAMES B. MCGRAW¹, JESSICA B. TURNER¹, SARA SOUTHER², CYNTHIA C. BENNINGTON³, MILAN C. VAVREK⁴, GAIUS R. SHAVER⁵ and NED FETCHER⁶

¹Department of Biology, West Virginia University, P. O. Box 6057 Morgantown, WV 26506-6057, USA, ²Department of Biology, West Virginia Wesleyan, Buckhannon, WV, USA, ³Department of Biology, Stetson University, DeLand, FL 32723, USA, ⁴Department of Land Resources, Glenville State University, Glenville, WV 26351, USA, ⁵The Ecosystems Center, Marine Biological Laboratory, Woods Hole, MA 02543, USA, ⁶Institute for Environmental Science and Sustainability, Wilkes University, Wilkes-Barre, PA 18766, USA

Abstract

Plants are often genetically specialized as ecotypes attuned to local environmental conditions. When conditions change, the optimal environment may be physically displaced from the local population, unless dispersal or *in situ* evolution keep pace, resulting in a phenomenon called adaptational lag. Using a 30-year-old reciprocal transplant study across a 475 km latitudinal gradient, we tested the adaptational lag hypothesis by measuring both short-term (tiller population growth rates) and long-term (17-year survival) fitness components of *Eriophorum vaginatum* ecotypes in Alaska, where climate change may have already displaced the optimum. Analyzing the transplant study as a climate transfer experiment, we showed that the climate optimum for plant performance was displaced ca. 140 km north of home sites, although plants were not generally declining in size at home sites. Adaptational lag is expected to be widespread globally for long-lived, ecotypically specialized plants, with disruptive consequences for communities and ecosystems.

Keywords: adaptational lag, Alaska, climate change, ecotype, *Eriophorum vaginatum*, latitudinal gradient

Received 7 January 2015; revised version received 7 January 2015 and accepted 19 May 2015

Introduction

In plants and other organisms with limited dispersal, natural selection frequently leads to genetically based ecotypic specialization, a phenomenon that has been studied experimentally for nearly a century (Turesson, 1922; Heslop-Harrison, 1964; Langlet, 1971; Linhart & Grant, 1996). Within a species, having a diverse array of ecotypes permits occupation of a much larger range of environments than any single set of genotypes could, effectively expanding the niche of that species (Joshi *et al.*, 2001). In a local environment, possessing adaptive 'specialist' traits allows ecotypes to compete successfully in the suite of environmental conditions found there (Linhart & Grant, 1996). Repeated demonstrations of home-site advantage in reciprocal transplant studies have led to ecotypic differentiation being considered the norm (Primack & Kang, 1989; Linhart & Grant, 1996; Anderson *et al.*, 2012), with lack of ecotypic differentiation being the exception for plants (Fetcher *et al.*, 2000).

The advantages of ecotypic specialization may vanish in a directionally changing environment (Holt, 1990; Davis & Shaw, 2001; Aitken *et al.*, 2008). Climate change represents one such set of directional changes, and in response, ecotypically differentiated populations must acclimate, adapt, migrate, or face possible extinction (Pease *et al.*, 1989, Davis & Shaw, 2001; Jump & Penuelas, 2005; Bell & Gonzalez, 2009; Souther & McGraw, 2011; Anderson *et al.*, 2012). Ecotypic specialization to the local environment, however, may limit the rate of possible adaptation, and if historical migration rates are an indication, dispersal may be too slow to keep up with a shifting environment (Davis & Shaw, 2001). Exceptions to this prediction could occur in disturbed environments where intermixing of ecotypes may be facilitated (McGraw *et al.*, 2014).

The net decline in absolute fitness due to inability to migrate or evolve fast enough to keep pace with climate change is termed 'adaptational lag' (Aitken *et al.*, 2008). Mismatches between ecotypes and environments would be expected to manifest themselves first where climate is changing rapidly. The most rapid growing season temperature increases are predicted for the Arc-

Correspondence: James B. McGraw, tel. 304-319-3225, fax 304-293-6363, e-mail: jmcgraw@wvu.edu

tic by general circulation models (IPCC 2014), and indeed, such changes have already been observed over the past 4–5 decades (Serreze *et al.*, 2000). Studies of ecological genetic variation and adaptational lag in the context of climate change are lacking for the Arctic (Anderson *et al.*, 2012).

Classical reciprocal transplant experiments provide an opportunity for a powerful test of the adaptational lag hypothesis because in the absence of climate change, home-site advantage would be expected. Alternatively, if the original home-site climate has been displaced northward, or to higher elevations, enhanced fitness might be expected for populations transplanted upward or northward, relative to plants transplanted back to their home sites. We took advantage of a 30-year-old Alaskan reciprocal transplant study in which home-site advantage was previously demonstrated (Shaver *et al.*, 1986; Bennington *et al.*, 2012) to test whether the optimum environment had indeed shifted northward for genetically distinct populations of a widespread Arctic plant, *Eriophorum vaginatum* L. A recent analysis of physiological traits of *E. vaginatum* in the transplant gardens supported the home-site advantage hypothesis for some traits (e.g., biomass per tiller), but the adaptational lag hypothesis for others (e.g., maximum photosynthetic rate; Souther *et al.*, 2014). In this study, we tested the home-site advantage hypothesis vs. adaptational lag hypothesis using two integrative measures of plant performance: (i) the population growth rate of tillers in the transplanted tussocks and (ii) whole-tussock survival over the course of the experiment.

Methods

Study system

Eriophorum vaginatum is a circumpolar tussock-forming sedge, and tussock tundra forms one of the dominant community types in mesic zones of the Arctic north of treeline (Walker *et al.*, 2005). Tussocks survive for over a century, and mature tussocks are composed of 300–600 tightly packed tillers (Fetcher & Shaver, 1982; Mark *et al.*, 1985). As with most long-lived perennial plants, individual seed production and survival are size-dependent (McGraw & Fetcher, 1992). Therefore, tiller population growth rate, which determines long-term size changes of individual tussocks, serves as an integrated measure of plant performance. Ultimately, when the tiller population within a tussock declines to zero, the tussock is dead. Therefore, tussock survival is also an integrated measure of performance in this long-lived perennial sedge, one that ultimately reflects many years of shoot population decline. We used both tiller population growth rate and tussock survival to

assess success of *Eriophorum vaginatum* ecotypes in the reciprocal transplant study.

Experimental procedures

In 1980, a reciprocal transplant study of five populations of *E. vaginatum* was established, with a sixth population and site added to the gardens in 1982 (Shaver *et al.*, 1986; Fetcher & Shaver, 1990), resulting in a complete factorial design (Fig. 1; six populations each transplanted to all six sites). Sites were selected from both north and south of the Brooks range, with the three northern locations at Toolik Lake (TL), Sagwon (SAG), and Prudhoe Bay (PB), and three sites south of the Brooks Range: Eagle Creek (EC), No Name Creek (NN), and Coldfoot (CF). The sites spanned a latitudinal gradient of five degrees and ranged in elevation from 8 to 770 m (Fetcher & Shaver, 1990). Ten tussocks from each of the six ecotypes were planted at each of the six sites, resulting in a total of 360 tussocks being transplanted (Shaver *et al.*, 1986; Fetcher & Shaver, 1990).

Tussocks were removed from the tundra at each site by slicing under the rhizomes with a serrated knife. At each transplant site, individuals were then placed in the precise location where a local tussock had been removed. The same transplant

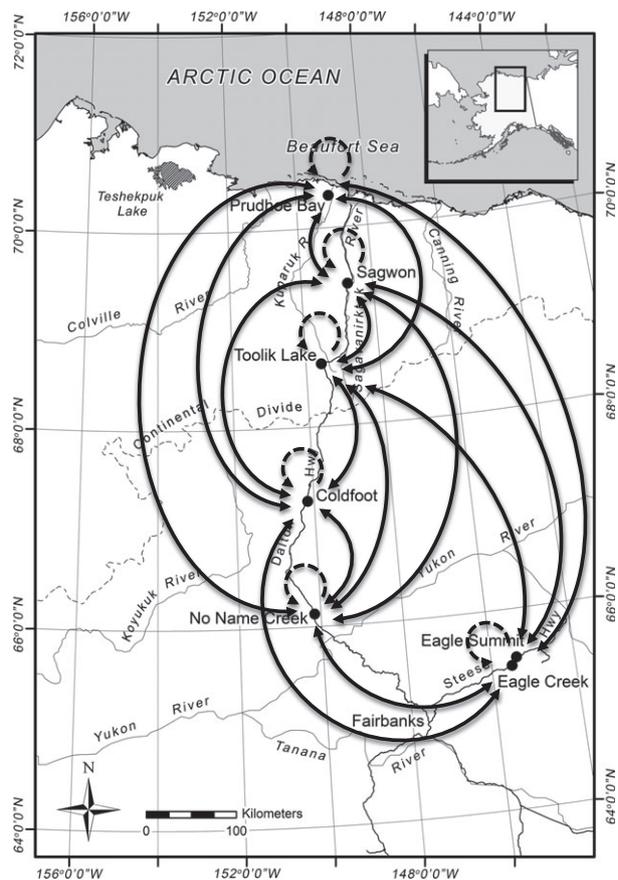


Fig. 1 Map showing experimental design of six populations reciprocally transplanted to six sites in northern Alaska. Dotted lines are transplant controls to the home site.

procedure was used for local tussocks as controls. *E. vaginatum* has deciduous roots, so while this procedure affected root function in the year of transplant, in subsequent years, new deciduous roots grew downward, anchoring the tussocks in place, restoring root function, and ensuring high transplant success (Fetcher & Shaver, 1990). No attempt was made to mitigate interactions with surrounding vegetation, thus ensuring as natural an introduction as possible. Reciprocally transplanted tussocks were censused in 1981–1983 and 1993.

Tiller population growth rate

In mid- to late July, 2010, all sites were visited again to census the tillers at peak leaf biomass. In all six gardens, we were able to unequivocally find 88% (316) of the original 360 tussocks. During this census, 12 tillers from each surviving tussock were haphazardly chosen to tag and census. If the entire tussock had 12 or fewer tillers, all of the surviving tillers were tagged. On each tiller, the two longest green leaves were measured and the number of green leaves was counted. In July of 2011, all of the tagged tillers on the transplanted tussocks were recensused in the field with the same methodology used in 2010. After field censusing, the tussocks were removed, brought to Toolik Field Station, and then dissected to count daughter shoots from the apical meristem of each tagged tiller (Fetcher & Shaver, 1990). These could be identified clearly as new shoots that lacked any leaf with a dead tip; the dead leaf tip being present only if the leaf was exposed over the previous winter (daughter tillers produced after July in a given year do not get large enough to show overwinter senescence). Only one census interval (July 2010 to July 2011) was used because the harvest was necessary to count daughter tillers and to discern where they originated.

Prior demographic work with *E. vaginatum* used age-based Leslie matrix models to project tiller population dynamics (Fetcher & Shaver, 1983). Most recently, this method was used for a subset of 12 of the 36 ecotype–site combinations in the reciprocal transplant study (Chandler *et al.*, 2015). However, demographic models structured by size or stage are often more appropriate to use with plants when mortality, growth, and reproduction are resource-limited (Werner & Caswell, 1977). The same principle holds at the level of the shoot module or tiller (McGraw & Antonovics, 1983; McGraw, 1989).

To create size classes, we first examined the allometric relationship between nondestructively measured tiller properties (leaf number and two leaf lengths) and leaf area. To do this, tillers from a variety of sizes and ecotypes were haphazardly selected from harvested tussocks, then the lengths of the two longest leaves were measured, and the numbers of leaves were counted on each tiller. Using an Epson Expression 836XL Scanner and Winfolia software, the total green leaf area of each tiller was calculated. An index (I) was created for each of the measured tillers by finding the product of the number of leaves and the sum of the length of the two longest leaves ($n = 66$). Measured tiller leaf area was regressed on the index to derive a predictive equation ($r^2 = 0.9448$) as follows:

$$\text{TillerLeafArea} = -8.447833 + 5.3464264(I) - 0.0056047(I)^2 \quad (1)$$

This equation was used to estimate tiller leaf area on all censused tillers in the reciprocal transplant gardens for both 2010 and 2011.

Tiller leaf area was used as the basis for size classes. To have accurate parameterization of the size classes, a distribution of log leaf area was produced for the 2011 data, and eight size-based stages were identified to ensure that each class had $N > 200$ tillers (Table 1). Each ecotype had tillers in each stage class as well. One additional stage class of tillers was daughter tillers (in 2010). The status of these tillers was inferred at harvest time in 2011 by their observed connection with tagged tillers and by the lack of any completely dead leaves (indicating they had originated in the prior year).

A total of 2934 tillers were included in the initial data set, as these tillers had measurements for 2010 and 2011, and had secure tags at the time of the harvest. Tillers were classified in the 2011 census as exhibiting one of three fates over the prior year: (i) died, (ii) survived and remained vegetative, or (iii) reproduced *via* vegetative tillering. ‘Death’ of a tiller was recognized when it retained no live leaves, regardless of the cause of death (e.g., flowering of the meristem or death of the meristem and subsequent loss of leaves). Death as a result of flowering occurred in <1% of tillers; thus, while flowering, if followed by seed production, could represent a positive contribution to overall population growth, this accounted for a small minority of tiller losses.

From the complete data set of stage transitions (all ecotypes in all sites) from 2010 to 2011, a 9×9 transition matrix (\mathbf{A}) was assembled (Caswell, 2001) and the finite rate of increase (λ) of the tiller population was calculated as the eigenvalue of \mathbf{A} using MATLAB. To obtain λ by ecotype and site within the transplant garden, we performed a variant of jackknifing we termed ‘Yellow Taxi Analysis’ (after the Joni Mitchell song containing the well-known verse ‘You don’t know what you’ve got til it’s gone’; Chandler *et al.*, 2015). This procedure judged the contribution of each tiller to population growth by removing it from the data set, determining a new matrix without that individual tiller (A_{-i}), and recalculating λ minus that tiller (λ_{-i}). This process was repeated for every tiller in all eco-

Table 1 Stage classes and corresponding size ranges (mm²). Stage class boundaries were approximately loglinear to produce comparably populated stage classes

Stage class	Size range	N (2011)	Stage class width
1	S1 (in 2010)	219	
2	$X \leq 100.49$	335	109.74
3	$100.49 < X \leq 174.78$	284	73.13
4	$174.78 < X \leq 248.83$	331	74.05
5	$248.83 < X \leq 329.96$	339	81.13
6	$329.96 < X \leq 427.57$	318	97.61
7	$427.57 < X \leq 539.34$	264	111.77
8	$539.34 < X \leq 699.13$	256	159.79
9	$699.13 < X$	230	720.97
10	Dead (in 2011)	364	

types in all gardens (2923 matrices, with 2923 values of λ_{-i}). Then, pseudovalues of lambda (Φ_i , for $i = 1$ to 2923) for each individual tiller were determined as follows (Eqn (2); Sokal & Rohlf, 2012):

$$\Phi_i = n\lambda_{\text{all}} - (n - 1)\lambda_{-i} \quad (2)$$

From this data set, the residuals for Φ_i , calculated as deviations from the ecotype–garden mean Φ_i value, were tested for outliers using Mahalanobis distance (SAS JMP Pro v. 11; SAS, Cary, NC, USA). A total of 69 tillers registered as outliers, but after examining the data, only eight tillers were removed, for a final $n = 2915$. Outliers were removed only in cases where the best explanation for the outlier was that the tag had slipped between years and had been replaced on the wrong tiller, or the tag had inadvertently been placed around two tillers in the prior year, leading to an incorrect size estimate in either case. The residuals deviated from normality slightly based on the powerful KSL test (SAS JMP Pro, v. 11; $P < 0.01$); however, the distribution was only minimally skewed right, while showing very slight leptokurtosis. In addition, Levene's test showed heteroscedasticity of residuals. No data transformation improved normality or homoscedasticity; thus, analyses were performed on untransformed data. ANOVA results are conditioned on the robustness to violations of these assumptions.

A 2-way ANOVA was performed on Φ_i with ecotype and transplant garden as main effects. The interaction term was included to determine whether ecotypes responded differentially to transplant gardens; tussock was nested as a random effect within the ecotype \times garden term. A second ANOVA was performed with each ecotype–garden combination recoded as home vs. away, and this location effect was tested over the nested random tussock term.

To determine whether the optimum climate had shifted, thaw degree-days (TDD) were determined for each garden. This integrated metric of season-long temperature differences was previously shown to be related to both physiological responses (Souther *et al.*, 2014) and tiller size (Shaver *et al.*, 1986). Mean thaw degree-days were calculated as the sum of mean air temperatures above 0 °C (Shaver *et al.*, 1986), but data for this study were from the SNOTEL weather station nearest to each transplant garden site for the period 2001–2011 (Souther *et al.*, 2014), adjusted for elevation differentials using the adiabatic lapse rate. These data were judged likely to be more accurate than the original stripchart data, and their primary purpose was to quantify TDD differences between sites.

The shift in TDD represented by each transplant treatment was determined as follows:

$$\Delta TDD = TDD_G - TDD_S, \quad (3)$$

where TDD_G represented the TDD of the transplant garden, and TDD_S was the TDD of the source population. Thus, a negative value of ΔTDD would be estimated for tussocks transplanted to a cooler climate, and positive values would occur for transplants to a warmer climate. We fitted a linear regression as well as second- or third-order polynomial regressions to a plot of mean Φ_i vs. ΔTDD , with the null expectation that if ecotypes remained locally adapted, the peak of the convex

polynomial fit should be at $\Delta TDD = 0$. However, if the optimal climate has shifted north (or up in elevation), then the peak would be at a negative value of ΔTDD . Fits of regressions were compared using adjusted AIC_c values.

To find the peak of the fitted curve, the first derivative of the polynomial was set equal to 0 and solved for ΔTDD . To determine whether an observed shift in optimum differed significantly from 0, the optimum was bootstrapped (Dixon, 2001) by drawing 1000 random samples from the data with replacement, performing 1000 regressions, and 1000 optimum calculations to find the exact probability that the geographic position of optimum TDD was <0 (i.e., north of the home site), as well as set confidence limits on the mean position of the optimum.

Tussock survival

Inventories of transplanted tussocks were performed in 1993 and 2010. Survival of tussocks was inferred by disappearances for the decade between 1983 and 1993, and then for the 17-year period between 1993 and 2010. At one site (NN), a fire burned the transplant garden area in 2004 and in the process burned a few stakes marking transplanted tussocks; therefore, at the 2010 census, we were less confident at that site that a disappearance between the two dates represented mortality. Hence, all observations at NN were deleted from the data set for the second interval.

A second-order logistic regression was performed with nominal tussock survival (Yes/No) as the dependent variable and ΔTDD as the independent variable to test for the existence of an optimum. This model was compared to the first-order model using AIC. The position of the TDD optimum for survival was tested against the null hypothesis of 0 using bootstrapping as described for tiller population growth rate above.

Results

Tiller population growth

Mean tussock growth rates, by ecotype and garden, were summarized by the mean pseudo-value for tiller population growth ($\bar{\Phi}$) of all tillers in each group. Expressed as a classical two-way reciprocal transplant garden analysis, the data appeared to support the home-site advantage hypothesis (Fig. 2). There was a differential response of ecotypes to gardens ($E \times G$ interaction; $F_{(25,238)} = 1.86$, $P = 0.0447$) and in all six gardens, the native ecotype at each garden ranked either first or second in tiller population growth rate. Moreover, with tillers recoded as 'home' vs. 'away', mean tiller population growth rates were marginally higher for 'home' populations across the experiment ($F_{(1,18)} = 2.82$, $P = 0.0582$). Nevertheless, these analyses do not explicitly examine whether the optimum is centered on a ΔTDD of 0, or alternatively whether the optimum is north of the home site.

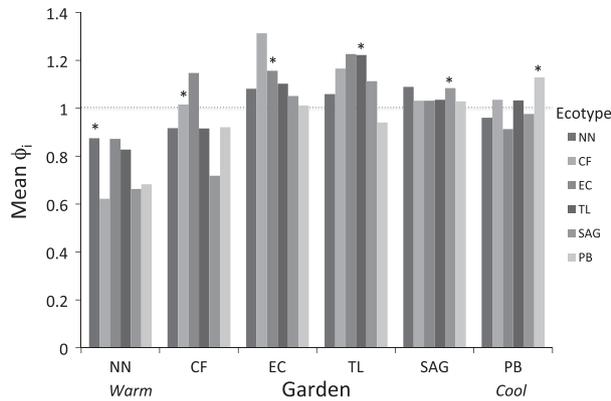


Fig. 2 Mean shoot population growth rates (ϕ_i) of six ecotypes of *Eriophorum vaginatum* in six transplant gardens in northern Alaska. Populations transplanted in home sites are marked with an asterisk (*).

To examine the position of the optimum, mean tiller population growth rates of each ecotype–garden combination were plotted against the change in growing season temperature represented by the transplant treatment (Fig. 3). The best-fit curve to the data was a second-order polynomial (by AIC_c), and the second-order term was negative ($t = -3.22$, $P = 0.0028$), yielding a convex surface. Moreover, the peak of the curve was significantly displaced to the north ($P < 0.001$; Fig. 3) at a $\Delta\text{TDD} = -362$ (95% confidence interval: LCL; -745 , UCL; -128), although the mean tiller population growth rate was still >1 (i.e., increasing) at a $\Delta\text{TDD} = 0$. In fact, tussocks were predicted to be growing (with $\phi_i > 1$) across a wide thaw degree-day difference range relative to home sites ($-1045 < \Delta\text{TDD} < +321$). The classical reciprocal transplant analysis shown in Fig. 2 suggested that all popu-

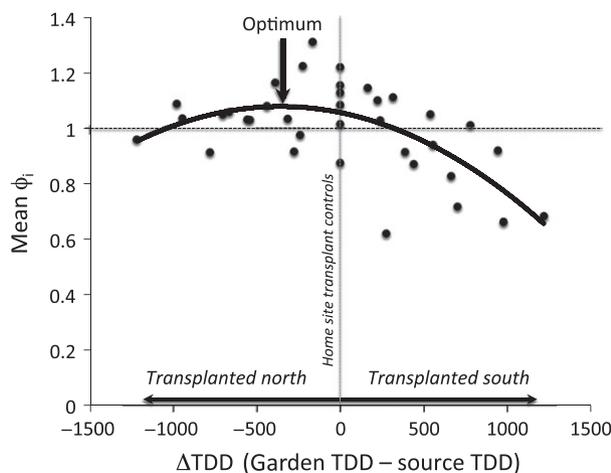


Fig. 3 Mean shoot population growth rate (ϕ_i) as a function of the thawing degree-day shift (Garden TDD – Source TDD) represented by each transplant treatment.

lations at the southernmost site (NN) were performing relatively poorly. Therefore, to determine whether this one site was responsible for the northward optimum shift, we excluded all data from this site and reformed the regression analysis. The results confirmed that even without this site in the analysis, the optimum tiller population growth rate was located north of the ‘home’ site (optimum $\Delta\text{TDD} = -231$).

Tussock survival

In the period from 1983 to 1993, only 6.3% of tussocks died in the whole reciprocal transplant study, and there was no pattern with respect to ΔTDD using either first-order (full model $\chi^2 = 0.0080$, $P = 0.9288$) or second-order logistic regression ($\chi^2 = 0.4677$, $P = 0.7915$). Between year 13 (1993) and year 30 (2010), overall survival of tussocks remained high (80%) for gardens that were censused at both times (note, however, one ‘extreme’ site (NN) could not be accurately censused over that interval). As with tiller population growth, tussock mortality exhibited a convex parabolic relationship to the change in thaw degree-days represented by each transplant, with an optimum located north of the home site at a location very close to that observed for tiller population growth (Fig. 4). A log transform was necessary to assure normality of the residuals of the jackknifed optimum pseudovalues, and after backtransformation, the mean optimum was $\Delta\text{TDD} = -366$ (LCL = -687 ; UCL = -187) and did differ significantly from 0 ($P < 0.001$). The shape of the logistic fit was relatively flat in the middle, such that the optimum sur-

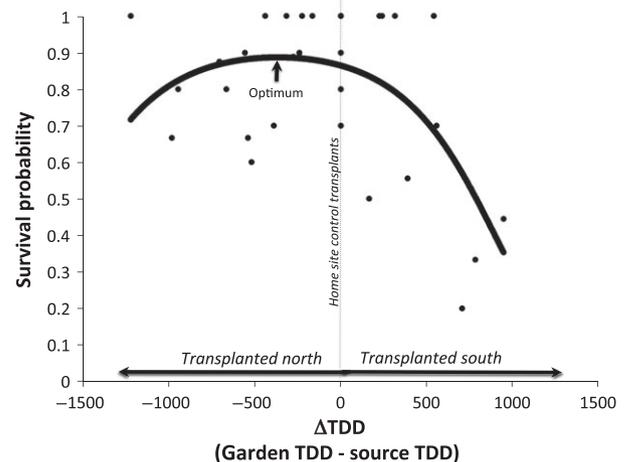


Fig. 4 Survival probability of tussocks in reciprocal transplant gardens between 1993 and 2010 as a function of thawing degree-day shift by each transplant treatment. The curve is the fit by second-order logistic regression, and the points represent actual proportions surviving in each ecotype–garden combination.

vival was only 2.6% higher than survival at the home site ($\Delta TDD = 0$).

Discussion

When the effect of thaw degree-days on the reciprocal transplants is not included, the results of this study seemed to support the 'home-site advantage' hypothesis. Indeed, prior work comparing home-site transplants to away-site transplants for the entire reciprocal transplant study concluded that the pattern of ecotypic differentiation and home-site advantage was generally supported (Bennington *et al.*, 2012; Souther *et al.*, 2014). This is consistent with the most common pattern shown by other studies of long-lived perennial plants both in the Arctic and elsewhere (Primack & Kang, 1989; McGraw & Fetcher, 1992; Linhart & Grant, 1996). The overall pattern of home-site advantage seen when comparing mean 'home' performance vs. 'away' performance, however, does not preclude the possibility that the optimum performance has shifted because the 'away' category of sites includes distant environments where performance may be especially poor.

Re-examining the same data set as a climate transfer experiment showed a subtle, but consistent deviation from home-site advantage. The northward location of the performance optimum suggests instead that populations of *E. vaginatum* may be experiencing 'adaptational lag' (Aitken *et al.*, 2008), in which the original home-site climate has moved, creating a mismatch between populations and their current environment. This interpretation makes several assumptions, including (i) that the sites chosen at each latitude were representative of such sites (only one site was chosen at each TDD level), (ii) that the transplanted populations were representative of genotypes found at that TDD level, and (iii) that the optimum was at $\Delta TDD = 0$ thirty years ago. In addition, the particular year in which shoot population growth was measured is assumed to be 'typical' of the recent climate. To test the latter assumption, we used SNOTEL data from three sites close to our transplant sites and compared the measurement year TDD to those same 1-year intervals in previous decade. We found that in fact, 2010–2011 was an average year, with a TDD within one standard deviation of the decadal mean at all sites.

The inference of adaptational lag could be limited if it relied solely upon short-term (1 year) shoot demography data. However, the interpretation is strengthened by its manifestation in both short-term (shoot population growth) and long-term (17-year tussock survival) measures of performance. This conclusion is further strengthened in light of the position of the optimum for maximum photosynthetic rates (A_{max}) reported previ-

ously ($\Delta TDD = -169.7$; Souther *et al.*, 2014), a measure of performance that is essentially instantaneous. In addition, Chandler *et al.* (2015), examining a subset of 12 population–site combinations in this experiment, showed a northward shift in shoot population growth based on an alternative age-specific Leslie matrix model. Thus, at three time scales (17 years, 1 year, and instantaneous) with two contrasting demographic analyses, the performance optimum was located north of the home site.

If the north-shifted optimum represents adaptational lag, how can its effects be quantified? The approach we reported here examined lag in terms of thaw degree-day distance. To put these values in perspective, the entire gradient from No Name Creek to Prudhoe Bay represented a difference of 1218 thaw degree-days. Sites were almost evenly spread across this gradient; thus, the optimum for shoot population growth was more than one site farther north than the home site. In terms of distance (ignoring elevational effects), the latitudinal gradient from No Name Creek to Prudhoe Bay is 475 km; thus, adaptational lag as measured by shoot population growth rate ($\Delta TDD = -362$) was the equivalent of ca. 141 km along the latitudinal gradient. Roughly quantifying adaptational lag in this manner emphasizes the magnitude of the dispersal challenge in maintaining a match between ecotype performance and the optimal climate.

Tempering the 'strong' adaptational lag interpretation of these data is the relatively small predicted drop-off in performance between the optimum and home-site positions along the gradient (2.6% and 2.1% drop for survival and tiller population growth, respectively). Mean tiller populations of tussocks transplanted to home sites were still growing ($\phi_i > 1$); thus, climate warming has not been so severe that local tussocks are, on average, declining in their home sites. An exception to this was observed at the warmest site (No Name), where home-site transplants and all others were declining. Indeed, this site showed signs of undergoing succession to boreal forest, with invasion of shrubs (*Salix* spp., *Betula* spp.) as well as spruce (*Picea mariana*). Home-site tussocks at the second-warmest site (CF) were growing only very slowly ($\phi_i = 1.015$, i.e., 1.5% per year), and young, growing spruce trees were abundant at that site as well, suggesting succession to boreal forest was underway. Range collapse at the warmer margin of the distribution is one predicted outcome of adaptational lag (Aitken *et al.*, 2008). Recent reports of shrub and tree expansion attributed to climate warming have been widespread in Alaska and the Arctic generally (Sturm *et al.*, 2001, 2005; Tape *et al.*, 2006, 2012). As *E. vaginatum* does have populations that

extend considerably farther south in isolated bogs and fens, these could be profitably examined for further evidence of southern margin population decline, although climate change has generally progressed more slowly at lower latitudes.

Performance of *E. vaginatum* tussocks transplanted south may predict the response to expected further climate warming in Alaska. The parabolic shapes of both performance vs. ΔTDD response curves suggest that even a linear increase in temperature in coming decades could result in an accelerated nonlinear drop in future performance, a pattern reflected in other widespread Arctic and alpine plants as well (Doak & Morris, 2010). Shoot populations begin to decrease in size ($\rho_i < 1$) when $\Delta\text{TDD} > +321$; that is, if climate warming is responsible for the optimum shift observed so far, the change is more than halfway to the point where tussocks will begin to decline. After 30 years, we observed that many south-transplanted tussocks in the gardens remained alive, but these individuals were comprised of mostly dead tillers, with only a few small green tillers remaining. Indeed, the slow loss of a viable tiller population, accompanied by invasion of mosses and vascular plants, appears to be the primary mechanism of tussock death (Fetcher & Shaver, 1982, 1983). In the absence of disturbance, recruitment of new tussocks is rare in closed tussock tundra (Gartner *et al.*, 1983); therefore, widespread tiller population decline could presage loss of tussock tundra at a site.

Theoretical predictions of adaptational lag have been made repeatedly (e.g., Holt, 1990; Davis & Shaw, 2001; Aitken *et al.*, 2008; Alberto *et al.*, 2013), but direct field tests have been few. Tor ng *et al.* (2015) demonstrated a classic pattern of local adaptation in a short-term reciprocal transplant study of *Arabis alpina* between Spain and Scandinavia, with no evidence of adaptational lag. The same pattern was observed for *Arabidopsis thaliana* when transplanted across a large latitudinal gradient from Sweden to Italy ( gren & Schemske, 2012). In both studies, differences in freezing tolerance appeared to be responsible for failure of southern genotypes to succeed in northern environments. However, Wilczek *et al.* (2014) compared response of *Arabidopsis thaliana* seed accessions from a wide array of environments in four common gardens in Europe, finding clear evidence for greater fitness of genotypes transplanted from farther south than the local genotypes, a pattern consistent with adaptational lag.

A major exception to the vacuum of information on population differences in response to climate change is the impressive body of literature on tree provenance plantations (reviewed in Savolainen *et al.*, 2007; Aitken *et al.*, 2008; and Alberto *et al.*, 2013). Most tree species

show signatures of local adaptation in such studies, but re-analyses of the growth data by relating performance to climate transfer functions have often demonstrated a pattern consistent with adaptational lag (e.g., for *Pinus contorta*: Rehfeldt *et al.*, 1999; Wang *et al.*, 2006).

Patterns observed in well-spaced and tended provenance plantations and common gardens may not reflect patterns in natural populations, due to reduced competition, and possibly lower herbivory and parasitism in those environments. In our study, *E. vaginatum* tussocks were transplanted whole and inserted into the community at each site in as natural a manner as possible. To our knowledge, this is the first study that has used a long-term reciprocal transplant study in a natural environment to test for adaptational lag. More such tests with additional species are needed to judge the ubiquity of adaptational lag, and these will be particularly valuable in northern latitudes where the climate has already changed substantially. Nevertheless, as a long-lived, locally specialized perennial plant, *E. vaginatum* is not unusual, and we predict that similar results would be expected for other species.

In the absence of gene flow, a long generation time, combined with negative genetic correlations among traits, makes *in situ* natural selection an unlikely mode of species rescue in the face of rapid climate change (Etterson & Shaw, 2001; Etterson, 2004; Savolainen *et al.*, 2007; Aitken *et al.*, 2008). Succession to alternative community dominants, such as shrubs or trees, could eliminate southern *E. vaginatum* populations unless there is sufficient within-population genetic variation accompanied by opportunities for establishment to counter the invasion. Northern populations could be spared this fate by the absence of alternative community dominants in the short term, but growth and productivity would be expected to decline nonetheless, a pattern projected for lodgepole pine in British Columbia *via* model simulations (O'Neill *et al.*, 2008).

Two natural processes could enhance gene flow from warmer to cooler climates, resulting in genetic rescue of a species such as *E. vaginatum*. First, *E. vaginatum* is wind-pollinated, as are many trees, and pollen can transport alleles related to success in warm climates farther than most seeds. In wind-pollinated trees, gene flow could introduce southern or low-elevation genes to higher elevation or northern populations over substantial distances (Anderson *et al.*, 2012). Second, increased rates of community disturbance, sometimes related to climate change itself, could allow enhanced opportunities for establishment of new genotypes (McGraw *et al.*, 2014), or resurrection of seeds stored deep in the seed bank (McGraw, 1993). In mesic Arctic tundra, such disturbances are likely to take the form of

increased fire frequency (Mack *et al.*, 2011) or thermokarst erosion (Schuur *et al.*, 2007). There is indirect genetic evidence for past long-distance dispersal events in Arctic tundra plants (Alsos *et al.*, 2007). Whether a sufficient number of such dispersal events, accompanied by establishment of new generations, can occur before climate change causes widespread extinction is not known.

This study did not have sufficient sample size of either populations or transplant gardens to examine the importance of factors other than temperature in relative transplant performance, but plants are often locally adapted to factors other than temperature (Anderson *et al.*, 2012). Studies with provenance plantations having a far greater number of source populations have shown that incorporating multiple factors can help make even better predictions of the spatial location of optimal future environments (St. Clair & Howe, 2007; Wang *et al.*, 2013). These studies acknowledge the possibility of ecological surprises such as forest pest outbreaks or change in fire regimes. In addition, no field-based studies have adequately accounted for possible differential effects of elevated CO₂ on ecotypes across a species' range.

The fact that fitness costs to climate change can be observed even after a relatively short and modest period of warming in Alaska suggests that adaptational lag will have even more important consequences for the abundance and distribution of *E. vaginatum* in the future. Such effects are expected to be widespread and disruptive in the Arctic for other species as well. Likewise, as similar climate changes occur at lower latitudes, the phenomenon can be expected to be widespread in locally adapted species there as well.

Acknowledgements

The authors thank Terry Chapin, Marjan Van de Weg, Jennifer Chandler, Zach Fowler, Timothy Fetcher, Caitlin Peterson, Melissa Shockey, Kayla Saxon, Rachel Burnett, Kelli Cummings, Hillary Tinney, and Verity Salmon for assistance with the field census and tussock pluck at Toolik Field Station. We thank Mark Burnham, Jennifer Chandler, and Chris Walter for comments on the manuscript. Thanks also to C-Q Zhang for assistance with derivatives of logistic fits. This research was supported by NSF grants ARC-0908936 to JBM and NF, and NSF grant PLR-1418010 to NF, James Tang, and Michael Moody.

References

Ågren J, Schemske D (2012) Reciprocal transplants demonstrate strong adaptive differentiation of the model organism *Arabidopsis thaliana* in its native range. *New Phytologist*, **194**, 1112–1122.

- Aitken SN, Yeaman S, Holliday JA, Wang T, Curtis-McLane S (2008) Adaptation, migration or extirpation: climate change outcomes for tree populations. *Evolutionary Applications*, **1**, 95–111.
- Alberto FJ, Aitken SN, Alia R *et al.* (2013) Potential for evolutionary responses to climate change – evidence from tree populations. *Global Change Biology*, **19**, 1645–1661.
- Alsos IG, Eidesen PB, Ehrlich D *et al.* (2007) Frequent long-distance plant colonization in the change Arctic. *Science*, **316**, 1606–1609.
- Anderson JT, Panetta AM, Mitchell-Olds T (2012) Evolutionary and ecological responses to anthropogenic climate change. *Plant Physiology*, **160**, 1728–1740.
- Bell G, Gonzalez A (2009) Evolutionary rescue can prevent extinction following environmental change. *Ecology Letters*, **12**, 942–948.
- Bennington CC, Fetcher N, Vavrek MC, Shaver GR, Cummings KJ, McGraw JB (2012) Home site advantage in two long-lived arctic plant species: results from two 30-year reciprocal transplant studies. *Journal of Ecology*, **100**, 841–851.
- Caswell H (2001) *Matrix Population Models*, 2nd edn. Sinauer, Sunderland.
- Chandler JL, McGraw JB, Bennington CC, Shaver GR, Vavrek MC, Fetcher N (2015) Tiller population dynamics of reciprocally-transplanted *Eriophorum vaginatum* L. ecotypes in a changing climate. *Population Ecology*, **57**, 117–126.
- Davis MB, Shaw RG (2001) Range shifts and adaptive responses to Quaternary climate change. *Science*, **292**, 673–679.
- Dixon P (2001) The bootstrap and the jackknife: describing the precision of ecological indices. In: *Design and Analysis of Ecological Experiments* (eds Scheiner SM, Gurevitch J), 2nd edn, pp. 267–288. Oxford University Press, Oxford.
- Doak DF, Morris WF (2010) Demographic compensation and tipping points in climate-induced range shifts. *Nature*, **467**, 959–962.
- Etterson JR (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**, 1446–1456.
- Etterson JR, Shaw RG (2001) Constraint to adaptive evolution in response to global warming. *Science*, **294**, 151–154.
- Fetcher N, Shaver GR (1982) Growth and tillering patterns within tussocks of *Eriophorum vaginatum*. *Holarctic Ecology*, **5**, 180–186.
- Fetcher N, Shaver GR (1983) Life histories of tillers of *Eriophorum vaginatum* in relation to tundra disturbance. *Journal of Ecology*, **71**, 131–147.
- Fetcher N, Shaver GR (1990) Environmental sensitivity of ecotypes as a potential influence on primary productivity. *The American Naturalist*, **136**, 126–131.
- Fetcher N, Corder RA, Voltzow J (2000) Lack of ecotypic differentiation: plant response to elevation, population origin, and wind in the Luquillo Mountains, Puerto Rico. *Biotropica*, **32**, 225–234.
- Gartner BL, Chapin FS III, Shaver GR (1983) Demographic patterns of seedling establishment and growth of native graminoids in an Alaskan tundra disturbance. *Journal of Applied Ecology*, **20**, 965–980.
- Heslop-Harrison J (1964) Forty years of genecology. *Advances in Ecological Research*, **2**, 159–247.
- Holt RD (1990) The microevolutionary consequences of climate change. *Trends in Ecology and Evolution*, **5**, 311–315.
- Intergovernmental Panel on Climate Change (2014) Climate Change 2014: Synthesis report. Summary for policy makers. Fifth assessment report, 133 pp., Copenhagen, Denmark.
- Joshi J, Schmid B, Caldeira MC *et al.* (2001) Local adaptation enhances performance of common plant species. *Ecology Letters*, **4**, 536–544.
- Jump AS, Penuelas J (2005) Running to stand still: adaptation and the response of plants to rapid climate change. *Ecology Letters*, **8**, 1010–1020.
- Langlet O (1971) Two hundred years of genecology. *Taxon*, **20**, 653–722.
- Linhart YC, Grant MC (1996) Evolutionary significance of local differentiation in plants. *Annual Review of Ecology, Evolution, and Systematics*, **27**, 237–277.
- Mack MC, Bret-Harte S, Hollingsworth TN *et al.* (2011) Carbon loss from an unprecedented Arctic tundra wildfire. *Nature*, **475**, 489–492.
- Mark AF, Fetcher N, Shaver GR, Chapin FS III (1985) Estimated ages of mature tussocks of *Eriophorum vaginatum* along a latitudinal gradient in central Alaska, U.S.A. *Arctic and Alpine Research*, **17**, 1–5.
- McGraw JB (1989) Effects of age and size on life histories and population growth of *Rhododendron maximum* shoots. *American Journal of Botany*, **76**, 113–123.
- McGraw JB (1993) Ecological genetic variation in seed banks. IV. Differentiation of extant and seed bank-derived populations of *Eriophorum vaginatum*. *Arctic and Alpine Research*, **25**, 45–49.
- McGraw JB, Antonovics J (1983) Experimental ecology of *Dryas octopetala* ecotypes. II. A demographic model of growth, branching, and fecundity. *Journal of Ecology*, **71**, 899–912.

- McGraw JB, Fetcher N (1992) Response of tundra plant populations to climatic change. In: *Arctic ecosystems in a changing climate: an ecophysiological perspective* (eds Chapin FS, Jefferies RL, Reynolds JF, Shaver GR, Svoboda J), pp. 359–376. Academic Press, New York, NY.
- McGraw JB, Turner JB, Chandler JL, Vavrek MC (2014) Disturbances as hot spots of genetic variation: a case study with ecotypes of *Dryas octopetala*. *Arctic, Antarctic, and Alpine Research*, **46**, 542–547.
- O'Neill GA, Hamann A, Wang T (2008) Accounting for population variation improves estimates of the impact of climate change on species' growth and distribution. *Journal of Applied Ecology*, **45**, 1040–1049.
- Pease CM, Lande R, Bull JJ (1989) A model of population growth, dispersal and evolution in a changing environment. *Ecology*, **70**, 1657–1664.
- Primack RB, Kang H (1989) Measuring fitness and natural selection in wild plant populations. *Annual Review of Ecology and Systematics*, **20**, 367–396.
- Rehfeldt GE, Ying CC, Spittlehouse DL, Hamilton DA (1999) Genetic responses to climate change in *Pinus contorta*: niche breadth, climate change, and reforestation. *Ecological Monographs*, **69**, 375–407.
- Savolainen O, Pyhajarvi T, Knurr T (2007) Gene flow and local adaptation in trees. *Annual Review of Ecology, Evolution and Systematics*, **38**, 595–619.
- Schuur EA, Crummer KG, Vogel JG, Mack MC (2007) Plant species composition and productivity following permafrost thaw and thermokarst in Alaskan tundra. *Ecosystems*, **10**, 280–292.
- Serreze MC, Walsh JE, Chapin FS *et al.* (2000) Observational evidence of recent change in the northern high-latitude environment. *Climate Change*, **46**, 159–207.
- Shaver GR, Fetcher N, Chapin FS (1986) Growth and flowering in *Eriophorum vaginatum*: annual and latitudinal variation. *Ecology*, **67**, 1524–1535.
- Sokal RR, Rohlf FJ (2012) *Biometry*, 4th edn. Freeman, New York, NY.
- Souther S, McGraw JB (2011) Local adaptation to temperature and its implications for species conservation in a changing climate. *Conservation Biology*, **25**, 922–931.
- Souther S, Fetcher N, Fowler Z, Shaver GR, McGraw JB (2014) Ecotypic differentiation in photosynthesis and growth of *Eriophorum vaginatum* L. along a latitudinal gradient in the Arctic tundra. *Botany-Botanique*, **92**, 551–561.
- St. Clair JB, Howe GT (2007) Genetic maladaptation of coastal Douglas-fir seedlings to future climates. *Global Change Biology*, **13**, 1441–1454.
- Sturm M, Racine C, Tape K (2011) Increasing shrub abundance in the arctic. *Nature*, **411**, 546–547.
- Sturm M, Schimel J, Michaelson G *et al.* (2005) Winter biological processes could help convert Arctic tundra to shrubland. *BioScience*, **55**, 17–26.
- Tape K, Sturm M, Racine C (2006) The evidence for shrub expansion in northern Alaska and the Pan-Arctic. *Global Change Biology*, **12**, 686–702.
- Tape KD, Hallinger M, Welker JM, Ruess RW (2012) Landscape heterogeneity of shrub expansion in Arctic Alaska. *Ecosystems*, **15**, 711–724.
- Toräng P, Wunder J, Obeso JR, Herzog M, Coupland G, Ågren J (2015) Large-scale adaptive differentiation in the alpine perennial herb *Arabis alpina*. *New Phytologist*, **206**, 459–470.
- Turesson G (1922) The species and variety as ecological units. *Hereditas*, **3**, 100–113.
- Walker DA, Reynolds MK, Daniëls FJ *et al.* (2005) The circumpolar Arctic vegetation map. *Journal of Vegetation Science*, **16**, 267–282.
- Wang T, Hamann A, Yanchuk A, O'Neill GA, Aitken SN (2006) *Global Change Biology*, **12**, 2404–2416.
- Wang T, O'Neill GA, Aitken SN (2013) Integrating environmental and genetic effects to predict responses of tree populations to climate. *Ecological Applications*, **20**, 153–163.
- Werner PA, Caswell H (1977) Population growth rates and age versus stage-distribution models for teasel (*Dipsacus sylvestris* Huds.). *Ecology*, **58**, 1103–1111.
- Wilczek AM, Cooper MD, Korves TM, Schmitt J (2014) Lagging adaptation to warming climate in *Arabidopsis thaliana*. *Proceedings of the National Academy of Sciences of the United States of America*, **111**, 7906–7913.