

Tiller population dynamics of reciprocally transplanted *Eriophorum vaginatum* L. ecotypes in a changing climate

Jennifer L. Chandler · James B. McGraw ·
Cynthia Bennington · Gaius R. Shaver ·
Milan C. Vavrek · Ned Fetcher

Received: 12 February 2014 / Accepted: 20 October 2014
© The Society of Population Ecology and Springer Japan 2014

Abstract Moist tussock tundra, dominated by the sedge *Eriophorum vaginatum* L., covers approximately 3.36×10^8 km² of arctic surface area along with large amounts of subarctic land area. *Eriophorum vaginatum* exhibits ecotypic differentiation along latitudinal gradients in Alaska. While ecotypic differentiation may be beneficial during periods of climate stability, it may be detrimental as climate changes, causing adaptational lag. Following harvest of a 30-year reciprocal transplant experiment, age-specific demographic data on *E. vaginatum* tillers were collected to parameterize a Leslie matrix. Yellow Taxi analysis, based on Tukey's Jackknife, was used to determine mean pseudo-values of tiller population growth rate ($\bar{\phi}_i$) for four source populations of *E. vaginatum* tussocks that were transplanted to each of three gardens along a latitudinal gradient. Source populations responded differentially along the latitudinal gradient. Survival and daughter tiller production influenced differences seen at the mid-latitude garden, and the overall

tiller population performance was generally improved by northward transplanting relative to southward transplanting. A comparison of home-source $\bar{\phi}_i$ and away-source $\bar{\phi}_i$ within the same transplant garden indicates no home-site advantage. Although populations were still growing when transplanted to home-sites ($\bar{\phi}_i = 1.056$), tiller population growth rate increased as Δ GDD became more negative relative to the home site (i.e., as tussocks were transplanted north). These results imply that populations are affected by climate gradients in a manner consistent with adaptational lag. This study documenting the response of high-latitude ecotypes to climate gradients may be an indication of the possible future effects of climate shift in more southern latitudes.

Keywords Adaptational lag · Climate change · Reciprocal transplant · Thermal niche · Weibull distribution · Yellow Taxi analysis

J. L. Chandler (✉) · J. B. McGraw
Department of Biology, West Virginia University, P.O. Box
6057, Morgantown, WV 26506-6057, USA
e-mail: jchandler23@gmail.com; jchandl8@mix.wvu.edu

C. Bennington
Department of Biology, Stetson University, Deland, USA

G. R. Shaver
Woods Hole Marine Biological Laboratory, Ecosystems Center,
Woods Hole, USA

M. C. Vavrek
Department of Land Resources, Glenville State College,
Glenville, USA

N. Fetcher
Biodiversity and Ecological Research Institute, Wilkes
University, Wilkes-Barre, USA

Introduction

The Northern Hemisphere, and Alaska's arctic tundra in particular, has experienced unprecedented climatic warming in recent centuries, and even in recent decades (Overpeck et al. 1997; Moberg et al. 2005; Sturm et al. 2005; Callaghan et al. 2010). Over the past 40–50 years, the arctic tundra has experienced local temperature increases of more than 0.5 °C per decade (Serreze et al. 2000; Sturm et al. 2005), and in accordance with the predictions of polar amplification by global circulation models, the rate of climatic warming will continue to be most extreme at higher latitudes (Manabe et al. 2011).

Climatic warming in northern latitudes leads to both abiotic and biotic changes in tundra ecosystems (Moritz

et al. 2002; Walker et al. 2006; Olofsson et al. 2009; Molau 2010). One type of tundra vegetation that could be affected by climate change in the arctic is moist tussock tundra (approximately 3.36×10^8 km², 2005 circumpolar arctic vegetation map; Walker et al. 2005; Molau 2010). The herbaceous tussock-forming sedge, *Eriophorum vaginatum* L., currently dominates moist tussock tundra (Fetcher and Shaver 1983). Although cold, the area dominated by *E. vaginatum* is climatically variable in terms of temperature and precipitation due to differences in elevation and latitude (Shaver et al. 1986; Hinzman et al. 2005), and this variation in climate is reflected in well-documented ecotypic variation of *E. vaginatum* (Bennington et al. 2012). Ecotypes are genetically differentiated populations within a species that have adapted to a specific set of environmental conditions (Montalvo and Ellstrand 2000; Hufford and Mazer 2003). As *E. vaginatum* ecotypes are exposed to stresses from climate change, local ecotypic differentiation, and the ineffectiveness of plasticity to compensate for climate shifts (Bennington et al. 2012), may result in the decline of *E. vaginatum* ecotypes in the arctic tundra.

Ecotypically differentiated plant populations are common throughout the arctic (Billings 1973; Chapin and Chapin 1981; McGraw and Antonovics 1983a, b; McGraw 1985a, b; Fetcher and Shaver 1990). *Eriophorum vaginatum* ecotypes exhibit marked morphological variation across environmental gradients (Shaver et al. 1986; Fetcher and Shaver 1990). Reciprocal transplant experiments revealed that *E. vaginatum* demonstrated differentiation in both growth and flowering along a latitudinal transect spanning from Eagle Creek, AK to Prudhoe Bay, AK (Shaver et al. 1986; Fetcher and Shaver 1990; Bennington et al. 2012). In addition, a 2010 census of *E. vaginatum* in the same reciprocal transplant gardens revealed differential mortality and reproduction of ecotypes within gardens, supporting an overall pattern of ecotypic differentiation among populations (Bennington et al. 2012).

Ecotypic differences within a species confer home-site advantage, in which local ecotypes have greater fitness in local environments relative to non-local ecotypes (Montalvo and Ellstrand 2000; Hufford and Mazer 2003). As a result, whereas ecotypic differentiation is advantageous to a plant in a relatively stable environment, when environmental conditions shift directionally, this specialization may prove disadvantageous (Davis and Shaw 2001; Jump and Penuelas 2005). This effect may be particularly acute when there is insufficient genetic variation within populations to respond to the shift, even though that variation may exist in other populations (Davis and Shaw 2001; Jump and Penuelas 2005; Souther and McGraw 2011). Further, even if the local variation existed, the longevity and low turnover of *E. vaginatum* tussocks in the populations may provide few opportunities for genetic change (McGraw and

Fetcher 1992). As warming in the northern hemisphere intensifies, ‘adaptational lag,’ which is a delayed evolutionary and migratory response of organisms to rapid climate change, may have far reaching negative effects on plant populations (Aitken et al. 2008), and the risk of extirpation in populations of tundra plants such as *E. vaginatum* may increase.

The purpose of this study was to determine whether the observed shifts in northern latitude climate patterns have already resulted in adaptational lag for *E. vaginatum* in northern Alaska, USA. The long-term persistence of plants in a reciprocal transplant study set up in 1980–1982 provides a unique opportunity to examine this question. Adaptational lag of ecotypes would be manifested as a consistent mismatch of ecotypes with local climate, such that tussocks from farther south were now performing better than local tussocks in a given transplant garden. Since individual *E. vaginatum* tussocks grow over decades through expansion of their tiller populations, we examined age-specific tiller birth and death rates to obtain an integrative measure of plant performance to gauge relative ecotype success.

Methods

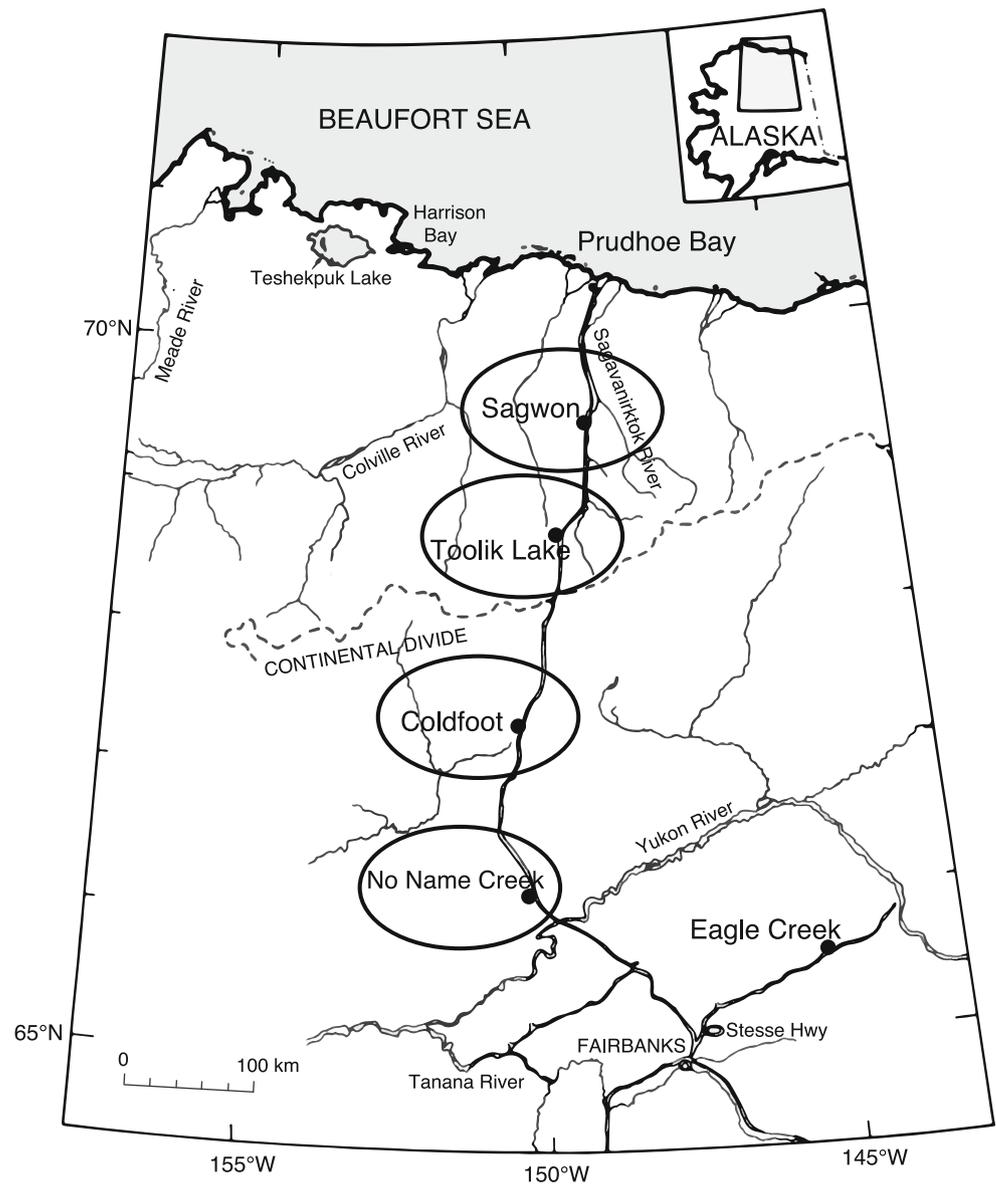
Study species

Eriophorum vaginatum is a long-lived, tussock-forming sedge (Mark et al. 1985), and a dominant member of many high latitude boreal wetlands and moist tundras (Walker et al. 2005; Bennington et al. 2012). Tussocks of *E. vaginatum* have modular construction in that they are comprised of clusters of repeating shoot modules (individual tillers) that may be viewed as populations within individuals (White 1979; Harper 1980; Watkinson and White 1986), and this study treats these modules in this manner. A single tussock of *E. vaginatum* is a tight aggregation of up to 600 live tillers (Fetcher and Shaver 1982). The annual rate of tiller population growth within each tussock yields an integrated measure of performance as it accounts for tiller birth and death rates (Fetcher and Shaver 1983; McGraw and Antonovics 1983b). Further, tiller population growth in *E. vaginatum* is linked to the present fitness in that as tiller population size increases so does overall tussock size, leading to increased reproductive output and increased chances of survival (McGraw and Wulff 1983; McGraw 1989; McGraw and Fetcher 1992).

Study sites

From 1980 to 1982, six reciprocal transplant gardens of *E. vaginatum* were established along a latitudinal gradient

Fig. 1 Map of latitudinal gradient showing approximate locations where reciprocal transplant gardens of *E. vaginatum* were established, with the three northern gardens (Sagwon, Toolik Lake, and Coldfoot) as focal gardens



stretching from just north of Fairbanks, Alaska, to Prudhoe Bay, Alaska (Shaver et al. 1986). Four of those populations were used in the present study, and three gardens (Coldfoot, Toolik Lake, and Sagwon) were chosen for in-depth study of tiller demography (Fig. 1; for further description of the original gardens, see Shaver et al. 1986). No Name Creek (NN) and Coldfoot (CF), the southernmost gardens, were located in openings in the boreal forest south of the Brooks Range, and Toolik Lake (TL) and Sagwon (SAG), the northernmost gardens, were located in tundra habitat north of the Brooks Range (Fig. 1).

In each source-garden combination, ten tussocks were transplanted, resulting in a total of 120 transplanted tussocks (4 source populations \times 3 gardens \times 10 tussocks per source-garden combination). Tussocks were

transplanted by slicing below the moss layer with a serrated knife and replanting the tussocks into the appropriate transplant garden (Shaver et al. 1986). The same procedure was used for tussocks transplanted to their home sites to control for transplant effects. *Eriophorum vaginatum* has deciduous roots that die back and re-grow each year from the rhizome bases of live tillers within the tussock (Bennington et al. 2012), therefore transplanting caused minimal damage to the tussocks.

Harvest

Of the original 120 tussocks transplanted, 99 were unequivocally located in 2010 (Bennington et al. 2012). Between July 13 and July 24, 2011, tussocks were removed

from the field for subsequent dissection. The destructive nature of tiller harvest precluded a multi-year analysis of tiller demography. However, these observations were not simply the result of 1 year of growth. Tiller growth, survival, flowering, and reproduction in any given year represent an integration of effects of multiple years of environmental conditions, including nutrient acquisition and storage (Shaver and Chapin 1995).

Census/analysis

Dead and living individual tillers were dissected and separated out of each tussock. If the tussock had fewer than 50 tillers, all tillers were processed as described below. For tussocks with a larger tiller population, a haphazardly chosen selection of tillers was processed as follows: For each tiller, the numbers of dead leaves, old live leaves (leaves with green bases, but with an over-wintered brown leaf tip), and new leaves (all green leaves with no over-wintered tip) were counted and used to estimate the age of each tiller. Although size-based matrix models are more commonly used, studies of the demography of shoot modules have shown that both size and age influence population growth rate (McGraw 1989). Following the precedent set by Fetcher and Shaver (1983) using this same species, age was used as a state variable in this experiment. In accordance with the methodology of Fetcher and Shaver (1983), tiller age was estimated by dividing total leaf number by the leaf production rate. Leaf production rate for each ecotype within each transplant garden was determined by finding the mean number of new leaves (per tiller) produced by all tillers within each tussock over one growing season. Leaf production rate was determined for each combination of ecotype and garden to account for both genetic and environmental variation, and was assumed constant across years in each of these combinations. Tillers that had brown, overwintered tips that did not produce any new leaves were considered “dead,” and were excluded from the calculation of leaf production rate to avoid biasing the estimate. The resulting tiller age estimate was a continuous variable, but each tiller was placed in an age class with a width of 1 year. For example, any tiller found to be between 2.0 and 2.999 years in age was placed in age class 2, between 3.0 and 3.999 years, age class 3, etc. Age class 0 and 1 tillers were aged as follows: Daughter tillers produced during the current growing season (age = 0) were distinguishable as ‘branches’ from the mother tiller with either white leaves or one or two small green leaves without a brown tip. Tillers produced during the prior growing season (age = 1) were distinguishable by the presence of one to two green leaves, one of which could have a brown tip, and by the absence of any completely dead leaves. In the rare instances when leaf types were not

able to be determined (e.g., due to grazing), the tiller was excluded from the data set. In total 3,305 tillers were aged in this study; an average of 275 tillers per ecotype-garden combination.

To calculate survival probabilities, haphazardly selected, recently dead tillers from all of the tussocks within each source population were aged by dividing total leaf number by the leaf production rate. The resulting age at death distribution was fit with Weibull distributions using the JMP 9.0 statistical program (SAS Institute, Inc. 2010). Weibull distributions are commonly used in engineering to model time-to-failure, and have been adopted by ecologists to summarize survivorship data (Pinder et al. 1978). Shape and scale parameters from each of the twelve Weibull distributions produced (4 populations \times 3 gardens) were used to derive a survival probability for the living tillers from each of the corresponding source populations at each garden. The survival function, which assumed a constant force of mortality over each interval of time from birth to death (Caswell 2001), was defined as:

$$l_x = e^{-\left(\frac{x}{z}\right)^\beta}$$

where l_x represents the age-specific probability of surviving from birth to age class (x), x represents the age class of the tiller being analyzed, and β and α represent the shape and scale parameters derived from each of the twelve Weibull distributions.

The l_x values for the living tillers in each of the twelve garden-source population combinations were then used to calculate the probability (p_x) of each tiller surviving from age x to age $x + 1$ using the formula:

$$p_x = \frac{l_{x+1}}{l_x}$$

To complete the Leslie matrix, the fertility (F_x) of individual living tillers was calculated using the formula:

$$F_x = m_x p_o$$

The total number of current year daughter tillers per mother (m_x) was determined for each tiller. Each dissected tiller was examined to determine if an individual tiller was a mother to vegetatively produced daughter tillers. Non-mother tillers were assigned an m_x value of zero. This vegetative demographic model did not include reproduction via seed because this type of reproduction is a very minor source of total *E. vaginatum* tiller population growth in the absence of disturbance (McGraw and Shaver 1982; Gartner et al. 1983).

Due to sample size limitations, one large Leslie matrix was formed for all of the tillers (3,305 in total) in the twelve source \times garden combinations, with age-specific fertilities (F_x) in the top row, and survival (p_x) in the subdiagonal. To determine the differential response of

populations to garden environments, replication is needed within each population-garden combination. To provide this replication, we carried out a ‘Yellow Taxi analysis’ (henceforth, YTA; McGraw 1989; Vavrek et al. 1996), which is a derivative of Tukey’s Jackknife that allows calculation of pseudovalues (ϕ_i) of the finite rate of increase of the population, λ . These pseudovalues measure each individual tiller’s (i) contribution to tiller population growth rate. To perform YTA, the fate of each individual (i), age x is assigned as (a) survived to the next age class, or (b) died, according to its age-specific survival probability (p_x). Each tiller is also assigned its observed fertility (F_x). A MATLAB program was then used to assemble Leslie matrices that include, and have all except, individual i . The population growth rate was then calculated with and without individual i from these matrices. Finally, the pseudovalue (ϕ_i) is calculated as an estimate of the missing individual’s contribution to overall tiller population growth as follows:

$$\phi_i = n\lambda_{all} - (n - 1)\lambda_{-i}$$

where n is the total number of individuals, λ_{-i} is the population growth rate with individual (i) removed and λ_{all} is the population growth rate with all individuals included (McGraw 1989; Vavrek et al. 1996, 1997).

To determine if tussocks from different sources responded differentially to transplanting along the latitudinal gradient, we performed a nested two-way ANOVA with ϕ_i as the dependent variable, garden and source population as main effects, and tussock as a nested random effect within the source \times garden interaction term. The Tukey–Kramer HSD a posteriori test was used to compare means.

Where large differences in mean tiller population growth rates ϕ_i were observed within gardens, we performed a life table response experiment (LTRE; Caswell 2001) to examine the underlying parameters controlling differences in growth rate. To do so, we formed individual matrices separately by population for a given garden, and due to small sample sizes in older age classes ($210 < n < 389$), the age-specific transition matrices were reduced to 11 age classes, with the last class being greater than or equal to 11 years of age. The LTRE was then used to compare pairs of matrices, attributing differences in overall λ for the matrices to components due to survival or fertility parameters (Caswell 2001);

$$\Delta\lambda_{ij} = (a_{ij,matrixA} - a_{ij,matrixB}) \times \frac{\partial\lambda}{\partial a_{ij}}$$

To determine if the tussocks that were transplanted back into their home site differed from those from other gardens, a second two-way ANOVA was performed with ϕ_i as the dependent variable, source population (re-coded as ‘home’ vs. ‘away’; Bennington et al. 2012) as the first independent

variable, garden as the second independent variable, and tussock (random effect) nested within the home/away \times garden interaction term. Data from the No Name Creek population were not included in this analysis, leaving a balanced design (3 populations \times 3 gardens) such that every population remaining would be both home and away in the design.

Along the climatic gradient represented by these three gardens, if a climate shift has occurred, we might expect the relative performance of home and away gardens to change along the gradient. To test whether the relative advantage of home-site tussocks changed as a function of growing degree-days, an ANCOVA was performed with the dependent variable being the mean pseudovalue of λ ($\bar{\phi}_i$) for each tussock, weighted by the total number of tillers in each tussock, home/away source as the first independent variable, and the degree-day difference from the southernmost garden (Coldfoot) as the second independent variable. As in the previous analysis, data from the No Name Creek population were not included in this analysis so that every population remaining would be both home and away in the design.

In order to determine the optimum environment for each source population, $\bar{\phi}_i$ for all tussocks (each tussock weighted by the total number of tillers in each tussock) for each of the twelve combinations of source and garden was regressed against the change in growing degree-days (Δ GDD) represented by each transplant. The growing degree-days (the summed daily mean air temperatures above 0 °C between May and September) described in Shaver et al. (1986) and Fetcher and Shaver (1990) were used to determine the shift in growing degree-days represented by each transplant within the experiment. To examine the effect of transplanting tussocks north vs. south of their original locations, we fit both linear and polynomial regression models (Y = tiller population growth, X = change in degree-days represented by the transplant). If there was consistent home-site advantage, we expected that the mean pseudovalues for the growth rate of tiller populations ($\bar{\phi}_i$) would be fit with a concave response surface with a maximum at zero (Fig. 2). If adaptational lag was evident, a shift of the optimum toward negative values of Δ GDD would be expected (Fig. 2; representing transplanting to the north) i.e., a negative overall slope of the regression of tiller population growth rates on change in GDD represented by each population-garden combination.

Results

A comparison of λ and $\bar{\phi}_i$ for all 3,305 tillers analyzed in this study confirmed that $\bar{\phi}_i$ provided an unbiased estimate of λ for the entire tiller population. The calculated value for

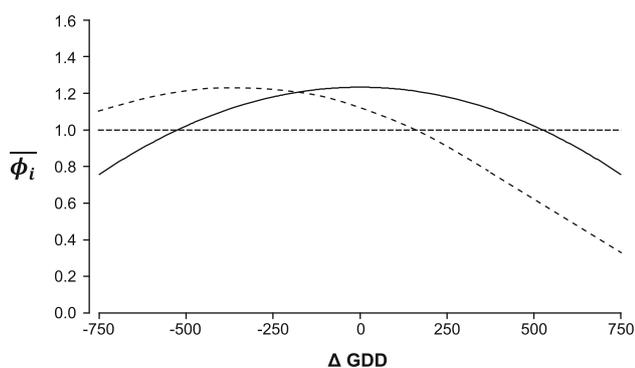


Fig. 2 The expected mean growth rate when a consistent home-site advantage is seen would exhibit optimum growth in the home garden, where $\Delta\text{GDD} = 0$ (solid line), and adaptational lag would be seen as a shift in the optimum toward negative values of ΔGDD , representing transplant northward (dashed line)

Table 1 (a) ANOVA showing the effect of Source population (CF, NN, TL, SAG) and Garden (CF, TL, SAG) on pseudovalues of growth rate of tiller populations (ϕ_i), (b) ANOVA showing the effect of Home vs. Away tussocks and Garden (CF, TL, SAG) on ϕ_i , and (c) ANCOVA showing the response of ϕ_i in Home vs. Away tussocks across the continuous growing degree-day gradient (measured by the change in degree-days from the southernmost garden)

Source of variation	df	SS	F	P
(a) Source population (S)	3	6.712	5.469	0.0013
Garden (G)	2	4.103	5.020	0.0077
S \times G	6	7.093	2.856	0.0117
Tussock (S \times G)	87	40.416	1.532	0.0013
Error	3,206	972.414		
(b) Source (Home vs. Away; S)	1	0.136	0.246	0.6211
Garden (G)	2	3.988	3.593	0.0317
S \times G	2	1.417	1.277	0.2841
Tussock (S \times G)	49	33.750	1.974	<0.0001
Error	2,369	826.586		
(c) Relative GDD difference	1	0.304	0.330	0.5675
Source (Home vs. Away; S)	1	0.492	0.534	0.4673
GDD \times S	1	2.002	2.173	0.1450
Error	70	64.521		

both λ and $\bar{\phi}_i$ was 1.082, meaning the entire tiller population would be growing at a rate of 8.2 % per year at a stable age distribution. Henceforth, we refer to $\bar{\phi}_i$ as the tiller population growth rate.

Populations responded differentially to transplanting along the latitudinal gradient (Table 1a). However no clear home-site advantage in tiller population growth rate was seen in any of the three transplant gardens (Fig. 3). The largest differences in tiller population growth rate among source populations were seen at Toolik Lake, the

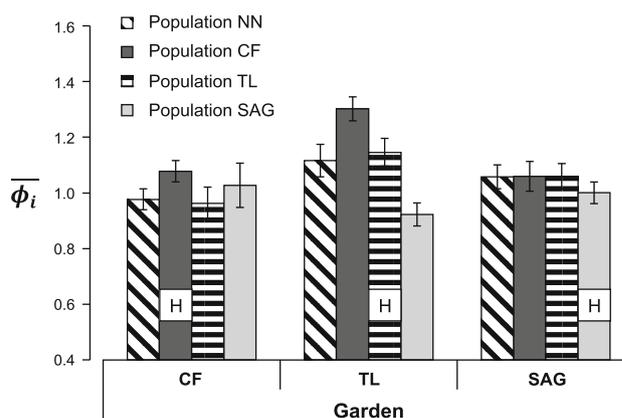


Fig. 3 The effect of transplant garden location on mean population growth rate ($\bar{\phi}_i$) as a function of source population. “H” designates home-site ecotype. (NN and CF = boreal forest; TL and SAG = tundra)

intermediate-latitude garden (Fig. 3). Generally, tussocks transplanted north into the Toolik Lake garden had improved tiller population growth rates, and the same trend was in the opposite direction for the northern population (SAG) that was moved south to Toolik (Fig. 3). Moreover, even the population from farthest south along the transect (NN) performed as well as the Toolik Lake population at Toolik Lake (Fig. 3). The net result was a large difference in growth among ecotypes at the Toolik site, with populations from warmer locations performing well there. No differences in tiller population growth rates were observed among the tussocks that were transplanted into the most southern and the most northern gardens (Fig. 3).

The LTRE analysis showed that the high population growth rate of southern CF tussocks at the Toolik garden, relative to the native TL tussocks, was entirely due to greater rates of new daughter tiller production by the CF tussocks ($\sum \Delta\lambda_{ij}$ for fertility matrix elements was 0.23 vs. -0.04 for the sum of survival matrix elements). By contrast, tillers from the northernmost SAG tussocks transplanted to Toolik performed poorly relative to the native TL tillers due to both lower tiller survival ($\sum \Delta\lambda_{ij} = 0.067$) and lower daughter tiller production ($\sum \Delta\lambda_{ij} = 0.090$). The large contrast in tiller population growth rate between northern SAG tussocks and southern CF tussocks at the Toolik garden was primarily due to higher rates of daughter tiller production by the CF tiller population ($\sum \Delta\lambda_{ij} = 0.332$), although nearly 20 % of the difference was also due to greater survival of southern CF tillers there.

Mean tiller population growth rate differed among gardens regardless of the source of the transplanted tussock (Table 1a). A Tukey–Kramer HSD test showed that the tussocks in the intermediate-latitude Toolik Lake garden had higher values of tiller population growth rate than the

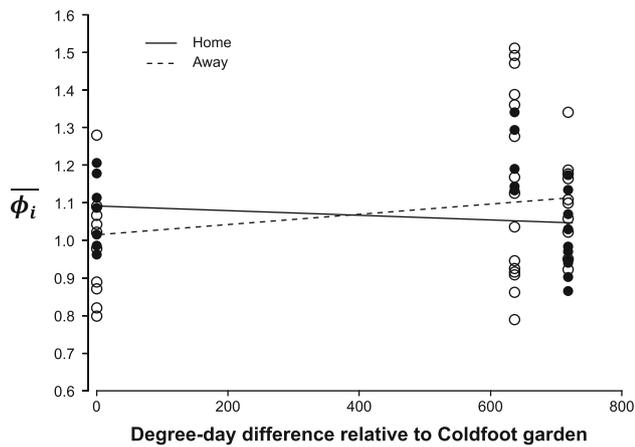


Fig. 4 Mean growth rate of tiller populations ($\bar{\phi}_i$) for home-source tussocks and away-source tussocks as a function of difference in growing degree-days. Although not significant, the pattern is consistent with expected response to adaptational lag. *Black circles* represent home-site tussocks, while *white circles* represent away-site tussocks. The *solid line* represents mean growth rate of tiller populations planted in their home environment, while the *dashed line* represents mean growth rate of tiller populations transplanted into non-home environments

tussocks in the lowest-latitude Coldfoot garden. Furthermore, tiller population growth rate differed among tussocks from different source populations, regardless of the garden into which they were transplanted (Table 1a). Overall, tussocks from the southern Coldfoot source had a higher value for tiller population growth rate than tussocks from the northern Sagwon source (Tukey–Kramer HSD), although clearly the interaction of Source and Garden complicates this interpretation (Table 1a).

Home tussocks and away tussocks did not respond differently to transplanting into gardens along the latitudinal gradient (Table 1b) and no home-site advantage was detected for any source population in any garden (Table 1b). As with the previous analysis, there was significant variation in tiller population growth rate among the three gardens analyzed (CF, TL, SAG; Table 1b), with the Toolik Lake garden having the highest tiller population growth rate (Tukey–Kramer HSD).

Relative tiller population growth rate of home vs. away tussocks did not respond differentially to the change in relative growing degree-days along the latitudinal transect (Table 1c). Though the observed pattern was consistent with what we would expect to see in response to climate change and adaptational lag (Fig. 4), the ANCOVA indicated that there was no significant difference in the relative performance of home vs. away tussocks as a function of growing degree-days.

Both a linear regression model (AIC = 246.49, $R^2_{adj} = 0.1417$) and a polynomial regression model (AIC = 247.35, $R^2_{adj} = 0.1442$) were fit to determine the

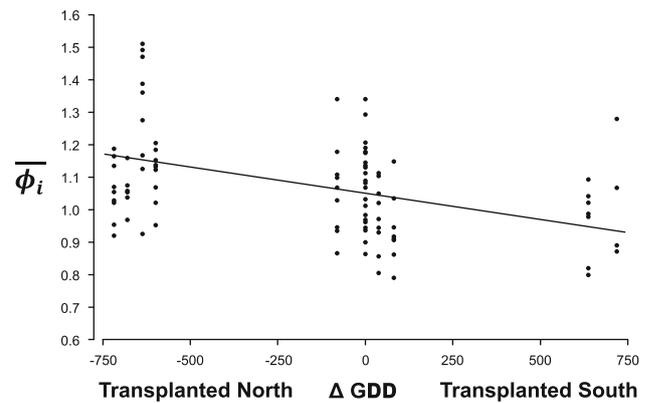


Fig. 5 Mean growth rate of tiller populations ($\bar{\phi}_i$) as a function of Δ GDD from home garden to transplant garden. Mean growth rate of tiller populations ($\bar{\phi}_i$), represented by a *solid line*, tended to increase as Δ GDD became more negative ($\beta = -0.000149$, $P < 0.0001$). Mean growth rate ($\bar{\phi}_i$) for all home-sites (Δ GDD = 0) was 1.056

effects of transplanting tussocks north vs. south, however the linear regression model was found to be a slightly better fit using AIC. Tiller population growth rate increased as Δ GDD became more negative (i.e., as tussocks were transplanted north Fig. 5; $\beta = -0.000149$, $P < 0.0001$). The growth rate predicted by the regression for home-sites (Δ GDD = 0) was 1.056, indicating that the tiller populations within tussocks were, on average, growing in size by 5.6 % per year (assuming a stable age distribution) at their home sites. However, tussocks had even higher average growth rates the farther north they were transplanted, as shown by the negative slope. The regression line predicts tiller numbers will decline (tiller population growth rate < 1) as Δ GDD becomes larger than 377, which would imply a shift to a warmer site.

Discussion

Eriophorum vaginatum was previously shown to exhibit ecotypic differentiation in Northern Alaska, USA (Shaver et al. 1986; Fetcher and Shaver 1990; Bennington et al. 2012). The purpose of the present study was to determine whether the observed shifts in arctic climate patterns have resulted in adaptational lag in *E. vaginatum* ecotypes. The response of tiller population growth rate to reciprocal transplanting provided important evidence that adaptational lag has already affected *E. vaginatum* ecotypes in Northern Alaska, with the most extreme responses in growth rate seen in the mid-latitude Toolik garden. Both survival and daughter tiller production influenced the differences seen at the Toolik garden, thus the overall performance of the tiller population was generally improved by northward transplanting relative to southward

transplanting, with the exception of transplantation into extreme northern gardens. In contrast to the 30-year pattern presented by the recent analysis of Bennington et al. (2012) that inferred a home-site advantage in terms of tussock survival, the current study showed no home-site advantage for the *E. vaginatum* ecotypes that were included. This suggests that a mismatch of ecotype and environment is presently occurring in tussock tundra. The differing results obtained in these two studies may be attributable to different time scales over which selection was measured. Bennington et al. (2012) focused on the net effect of 30 years of differential survival of *E. vaginatum*, however the tiller dynamics we measured likely reflects only the recent, warmer climate conditions of interior Alaska. The results of Bennington et al. (2012) included effects of earlier years when ecotype performance was likely more closely matched to the climate at each garden. However, Bennington et al. (2012) also found that a different pattern of tussock survival has been detected only since 1993, where tussocks transplanted northward survived at higher rates than tussocks transplanted southward. This more recent pattern detected by Bennington et al. (2012) supports our findings.

We hypothesized that relative tiller population growth rates of home-site tussocks would change as a function of growing degree-days (Fig. 4), and although the results followed this trend, the pattern was not statistically significant ($F = 2.173$, $P = 0.1450$). Current growth rates of home-site tussocks are not changing as a function of growing degree-days, however this may be due to the fact that the changes are not pronounced enough to be detected currently. Additionally, significant effects may have been detectable had the analysis included more source-garden combinations.

Although the regression of tiller population growth on change in growing degree-days represented by the transplant supports the hypothesis that adaptational lag is already occurring, the environment has not changed so much that home site tussocks are showing negative population growth rates. Mean growth rate of tiller populations for all home sites ($\Delta\text{GDD} = 0$) was 1.056. The regression slope does imply, however, that with further warming, tiller population growth will begin to decline, which would ultimately result in lower tussock reproduction and survival.

Rapid, continued climatic shift may result in population decline and possible mortality in ecotypes if such ecotypes lack the plasticity required to respond rapidly to the changing environment (Bell 2012). However, this transplant study indicates that as the climate shifts and warming continues in high latitudes, ecotypes from farther south may be able to thrive in more northern locations. The success or failure of these ecotypes will depend largely on

opportunities for range expansion. Although *E. vaginatum* can reproduce via seed dispersal and germination (McGraw and Shaver 1982; Gartner et al. 1983), recruitment from seed is rare in the absence of disturbances such as frost-heaving or fire (Fetcher and Shaver 1982). *Eriophorum vaginatum* seeds are capable of long-distance dispersal (Bennington et al. 2012), however, successful establishment of new populations in far northern latitudes may be limited due to physical barriers such as the extensive closed-canopy boreal forest and high mountain ranges that fragment tussock habitat. Several authors (Sturm et al. 2001, 2005; Tape et al. 2006; Myers-Smith et al. 2011) described a shift in species composition from tussock tundra to deciduous shrub with the onset of increasing temperature. If tiller populations begin to decrease, the tussocks will likely be invaded by mosses and shrubs (Fetcher and Shaver 1983), accelerating a community shift to an alternate state.

Ecotypically differentiated plant populations are plentiful in the arctic, but need not rely on such large-scale environmental variation. For example, the arctic dwarf shrub *Dryas octopetala* L. clearly shows ecotypic variation over a scale of meters (McGraw and Antonovics 1983a; Bennington et al. 2012), relative to a scale of kilometers in our study. In a reciprocal transplant study, populations of *D. octopetala* showed large site-specific variations in morphology and fitness across an elevation gradient from snowbank to fellfield (McGraw and Antonovics 1983a; McGraw 1987). Another example of the response of *Dryas* to variations in the environment is the early onset of flowering and increases in the abundance of flowers in *Dryas* grown in locations undergoing early snowmelt (Høye et al. 2007). If southern ecotypes of *E. vaginatum* and other species found throughout tussock tundra are not able to shift their spatial location northward or higher in elevation, it is possible that the species will decline in abundance and changes in community structure may follow.

The climatic change that has occurred so far is not a threat to the population growth of *E. vaginatum* within our study sites (growth rate at home-site >1), however, there is no assurance that growth rates will remain positive if the optimum shifts farther north from these home-sites. Although this study has focused solely upon Alaska's tussock tundra, the study has important implications. Climate shifts are most rapid at northern latitudes, and as such, adaptational lags are likely to manifest themselves first in these regions; however, similar threats of adaptational lag and population declines in locally adapted populations are likely to spread to southern latitudes with time.

Acknowledgments For their hard work in and out of the field, we thank Drs. Terry Chapin and Marjan van de Weg, WVU graduate

researcher Jessica Brie Turner, and undergraduate researchers Rachel Burnett, Kayla Saxon, and Hillary Harold. We would like to thank the Toolik Lake Field Station and the Arctic LTER project (NSF-DEB-1026843) for logistical support. This study was funded by the National Science Foundation (ARC-0908936).

References

- Aitken SN, Yeaman S, Holliday JA, Wang T, Curtis-McLane S (2008) Adaptation, migration or extirpation: climate change outcomes for tree populations. *Evol Appl* 1:95–111
- Bell G (2012) Evolutionary rescue and the limits of adaptation. *Philos Trans R Soc B Biol Sci* 368:1–6
- 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. *J Ecol* 100:841–851
- Billings WD (1973) Arctic and alpine vegetations: similarities, differences, and susceptibility to disturbance. *Bioscience* 23:697–704
- Callaghan TV, Bergholm F, Christensen TR, Jonasson C, Kokfelt U, Johansson M (2010) A new climate era in the sub-arctic: accelerating climate changes and multiple impacts. *Geophys Res Lett* 37:1–6
- Caswell H (2001) Matrix population models: construction, analysis, and interpretation, 2nd edn. Sinauer Associates, Sunderland
- Chapin FS III, Chapin MC (1981) Ecotypic differentiation of growth processes in *Carex aquatilis* along latitudinal and local gradients. *Ecology* 62:1000–1009
- Davis MB, Shaw RG (2001) Range shifts and adaptive responses to quaternary climate change. *Science* 292:673–679
- Fetcher N, Shaver GR (1982) Growth and tillering patterns within tussocks of *Eriophorum vaginatum*. *Holarct Ecol* 5:180–186
- Fetcher N, Shaver GR (1983) Life histories of tillers of *Eriophorum vaginatum* in relation to tundra disturbance. *J Ecol* 71:131–147
- Fetcher N, Shaver GR (1990) Environmental sensitivity of ecotypes as a potential influence on primary productivity. *Am Nat* 136:126–131
- Gartner BL, Chapin FS III, Shaver GR (1983) Demographic patterns of seedling establishment and growth of native graminoids in an Alaskan tundra disturbance. *J Appl Ecol* 20:965–980
- Harper JL (1980) Plant demography and ecological theory. *Oikos* 35:244–253
- Hinzman LD, Bettez ND, Bolton WR, Chapin FS, Dyrugerov MB, Fastie CL, Griffith B, Hollister RD, Hope A, Huntington HP, Jensen AM, Jia GJ, Jorgenson T, Kane DL, Klein DR, Kofinas G, Lynch AH, Lloyd AH, McGuire AD, Nelson FE, Oechel WC, Osterkamp TE, Racine CH, Romanovsky VE, Stone RS, Stow DA, Sturm M, Tweedie CE, Vourlitis GL, Walker MD, Walker DA, Webber PJ, Welker JM, Winker KS, Yoshikawa K (2005) Evidence and implications of recent climate change in northern Alaska and other arctic regions. *Clim Change* 72:251–298
- Høye TT, Ellebjerg SM, Philipp M (2007) The impacts of climate on flowering in the high arctic: the case of *Dryas* in a hybrid zone. *Arct Antarct Alp Res* 39:412–421
- Hufford KM, Mazer SJ (2003) Plant ecotypes: genetic differentiation in the age of ecological restoration. *Trends Ecol Evol* 18:147–155
- Jump AS, Penuelas J (2005) Running to stand still: adaptation and the response of plants to rapid climate change. *Ecol Lett* 8:1010–1020
- Manabe S, Ploshay J, Lau NC (2011) Seasonal variation of surface temperature change during the last several decades. *J Clim* 24:3817–3821
- 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, USA. *Arct Antarct Alp Res* 17:1–5
- McGraw JB (1985a) Experimental ecology of *Dryas octopetala* ecotypes: relative response to competitors. *New Phytol* 100:233–241
- McGraw JB (1985b) Experimental ecology of *Dryas octopetala* ecotypes. III. Environmental factors and plant growth. *Arct Antarct Alp Res* 17:229–239
- McGraw JB (1987) Experimental ecology of *Dryas octopetala* ecotypes IV. Fitness response to reciprocal transplanting in ecotypes with differing plasticity. *Oecologia* 73:465–468
- McGraw JB (1989) Effects of age and size on life histories and population growth of *Rhododendron maximum* shoots. *Am J Bot* 76:113–123
- McGraw JB, Antonovics J (1983a) Experimental ecology of *Dryas octopetala* ecotypes I. Ecotypic differentiation and life-cycle stages of selection. *J Ecol* 71:879–897
- McGraw JB, Antonovics J (1983b) Experimental ecology of *Dryas octopetala* ecotypes II. A demographic model of growth, branching and fecundity. *J Ecol* 71:899–912
- McGraw JB, Fetcher N (1992) Response of tundra plant populations to climatic change. In: Chapin FS, Jeffries RL, Reynolds JF, Shaver GR, Svoboda J (eds) Arctic ecosystems in a changing climate. Academic Press, New York, pp 359–376
- McGraw JB, Shaver GR (1982) Seedling density and seedling survival in Alaskan cotton grass tussock tundra. *Holarct Ecol* 5:212–217
- McGraw JB, Wulff RD (1983) The study of plant growth: a link between the physiological ecology and population biology of plants. *J Theor Biol* 103:21–28
- Moberg A, Sonechkin DM, Holmgren K, Datsenko NM, Karlén W (2005) Highly variable Northern Hemisphere temperatures reconstructed from low-and high-resolution proxy data. *Nature* 433:613–617
- Molau U (2010) Long-term impacts of observed and induced climate change on tussock tundra near its southern limit in northern Sweden. *Plant Ecol Divers* 3:29–34
- Montalvo AM, Ellstrand NC (2000) Transplantation of the Subshrub *Lotus scoparius*: testing the home-site advantage hypothesis. *Conserv Biol* 14:1034–1045
- Moritz RE, Bitz CM, Steig EJ (2002) Dynamics of recent climate change in the arctic. *Science* 297:1497–1502
- Myers-Smith IH, Forbes BC, Wilming M, Hallinger M, Lantz T, Blok D, Tape KD, Macias-Fauria M, Sass-Klaassen U, Lévesque E, Boudreau S, Ropars P, Hermanutz L, Trant A, Collier LS, Weijers S, Rozema J, Rayback SA, Schmidt NM, Schaepman-Strub G, Wipf S, Rixen C, Ménard CB, Venn S, Goetz S, Andreu-Hayles L, Elmendorf S, Ravolainen V, Welker J, Grogan P, Epstein HE, Hik DS (2011) Shrub expansion in tundra ecosystems: dynamics, impacts and research priorities. *Environ Res Lett* 6:045509
- Olofsson J, Oksanen L, Callaghan T, Hulme PE, Oksanen T, Suominen O (2009) Herbivores inhibit climate-driven shrub expansion on the tundra. *Glob Change Biol* 15:2681–2693
- Overpeck J, Hughen K, Hardy D, Bradley R, Case R, Douglas M, Finney B, Gajewski K, Jacoby G, Jennings A, Lamoureux S, Lasca A, MacDonald G, Moore J, Retelle M, Smith S, Wolfe A, Zielinski G (1997) Arctic environmental change of the last four centuries. *Science* 278:1251–1256
- Pinder JE III, Wiener JG, Smith MH (1978) The Weibull distribution: a new method of summarizing survivorship data. *Ecology* 59:175–179
- SAS Institute, Inc. (2010) SASJMP statistical discovery software. Version 9.0. Cary, North Carolina

- Serreze MC, Walsh JE, Chapin FS, Osterkamp T, Dyurgerov M, Romanovsky V, Oechel WC, Morison J, Zhang T, Barry RG (2000) Observational evidence of recent change in the northern high-latitude environment. *Clim Change* 46:159–207
- Shaver GR, Chapin FS (1995) Alaskan wet and moist tundra sedge species. *Ecography* 18:259–275
- Shaver GR, Fetcher N, Chapin FS (1986) Growth and flowering in *Eriophorum vaginatum*: annual and latitudinal variation. *Ecology* 67:1524–1535
- Souther S, McGraw JB (2011) Evidence of local adaptation in the demographic response of American ginseng to interannual temperature variation. *Conserv Biol* 25:922–931
- Sturm M, Racine C, Tape K (2001) Increasing shrub abundance in the arctic. *Nature* 411:546–547
- Sturm M, Schimel J, Michaelson G, Welker JM, Oberbauer SF, Liston GE, Fahnestock J, Romanovsky VE (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. *Glob Change Biol* 12:686–702
- Vavrek MC, McGraw JB, Yang HS (1996) Within-population variation in demography of *Taraxacum officinale*: maintenance of genetic diversity. *Ecology* 77:2098–2107
- Vavrek MC, McGraw JB, Yang HS (1997) Within-population variation in demography of *Taraxacum officinale*: season- and size-dependent survival, growth and reproduction. *J Ecol* 84:277–287
- Walker DA, Raynolds MK, Daniëls FJ, Einarsson E, Elvebakk A, Gould WA, Katenin AE, Kholod SS, Markon CJ, Melnikov ES, Moskalenko NG, Talbot SS, Yurtsev BA (2005) The circumpolar arctic vegetation map. *J Veg Sci* 16:267–282
- Walker MD, Wahren CH, Hollister RD, Henry GHR, Ahlquist LE, Alatalo JM, Bret-Harte MS, Calef MP, Callaghan TV, Carroll AB, Epstein HE, Jónsdóttir IS, Klein JA, Magnússon B, Molau U, Oberbauer SF, Rewa SP, Robinson CH, Shaver GR, Suding KN, Thompson CC, Tolvanen A, Totland Ø, Turner PL, Tweedie CE, Webber PJ, Wookey PA (2006) Plant community responses to experimental warming across the tundra biome. *Proc Natl Acad Sci* 103:1342–1346
- Watkinson AR, White J (1986) Some life-history consequences of modular construction in plants. *Philos Trans R Soc B Biol Sci* 313:31–51
- White J (1979) The plant as a metapopulation. *Annu Rev Ecol Syst* 10:109–145