Home site advantage in two long-lived arctic plant species: results from two 30-year reciprocal transplant studies

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Summary
1. Reciprocal transplant experiments designed to quantify genetic and environmental effects on phenotype are powerful tools for the study of local adaptation. For long-lived species, especially those in habitats with short growing seasons, however, the cumulative effects of many years in novel environments may be required for fitness differences and phenotypic changes to accrue.

2. We returned to two separate reciprocal transplant experiments thirty years after their initial establishment in interior Alaska to ask whether patterns of differentiation observed in the years immediately following transplant have persisted. We also asked whether earlier hypotheses about the role of plasticity in buffering against the effects of selection on foreign genotypes were supported. We censused survival and flowering in three transplant gardens created along a snowbank gradient for a dwarf shrub (Dryas octopetala) and six gardens created along a latitudinal gradient for a tussock-forming sedge (Eriophorum vaginatum). For both species, we used an analysis of variance to detect fitness advantages for plants transplanted back into their home site relative to those transplanted into foreign sites.

3. For D. octopetala, the original patterns of local adaptation observed in the decade following transplant appeared even stronger after three decades, with the complete elimination of foreign ecotypes in both fellfield and snowbed environments. For E. vaginatum, differential survival of populations was not evident 13 years after transplant, but was clearly evident 17 years later. There was no evidence that plasticity was associated with increased survival of foreign populations in novel sites for either D. octopetala or E. vaginatum.

4. Synthesis. We conclude that local adaptation can be strong, but nevertheless remain undetected or underestimated in short-term experiments. Such genetically based population differences limit the ability of plant populations to respond to a changing climate.

Key-words: adaptation, Dryas octopetala, ecological genetics and ecogenomics, Eriophorum vaginatum, genetic differentiation, phenotypic plasticity, tussock tundra

Introduction

Genetic differentiation among plant populations in response to selection on morphological, phenological and physiological characters has resulted in locally adapted genotypes, or ecotypes, across narrow to broad spatial scales. Ecotypes may form over short distances in response to edaphic characteristics (e.g. Bennington & McGraw 1995; Brady, Kruckeberg & Bradshaw 2005; Knight et al. 2006; Sambatti & Rice 2006; Wright 2007; Hufford, Mazer & Camara 2008), biotic interactions (e.g. Liancourt & Tielborger 2009) or topographic features (e.g. Byars, Pupst & Hoffmann 2007; Gonzalo-Turpin & Hazard 2009), while multiple factors, including climate, may result in such differentiation on larger scales (e.g. Chapin & Chapin 1981; Joshi et al. 2001; Rutter & Fenster 2007). While ecotypic specialization confers a fitness advantage relative to
other genotypes in the local environment, maladaptation of foreign genotypes could inhibit their invasion into new environments (Hereford 2009). Genotypes that exhibit phenotypic plasticity, and hence have an extensive niche breadth, may have greatest success in novel environments (Bradshaw 1965; Van Valen 1965; Sultan & Spencer 2002; Richards et al. 2006). Although phenotypic plasticity and genetic differentiation have been described as alternate solutions for coping with environmental variability (Schlichting 1986; Levin 1988), there is growing evidence that phenotypic plasticity may facilitate genetic differentiation in response to environmental variability (e.g. Schlichting 2004; West-Eberhard 2005; Pilgucci 2007; Pfennig et al. 2010). This is true if plastic responses increase survival of genotypes across environments, and expose individuals to natural selection that favours a genetic response in the same direction as the phenotypic one (e.g. Crispo 2007). Thus, predictions about the ability of populations to expand their range or cope with environmental change depend upon an estimation of the degree of both genetic differentiation and phenotypic plasticity (e.g. Nicotra et al. 2010; Hendry et al. 2011).

Reciprocal transplant experiments have been used extensively to quantify the relative magnitude of environmental and genetic influences on plant phenotype (Primack & Kang 1989; Linhart & Grant 1996). In arctic and alpine systems, reciprocal transplant experiments conducted over exposure and/or elevational gradients (e.g. Clausen, Keck & Hiesey 1940, 1948; McGraw & Antonovics 1983a,b; Galen, Shore & Deyoe 1991; Shimono et al. 2009) as well as latitudinal gradients (e.g. Chapin & Chapin 1981; Shaver, Fetcher & Chapin 1986; Fetcher & Shaver 1990) have demonstrated genetic differentiation in morphological and physiological traits. In some cases, clear evidence for local adaptation has been found even in the face of potentially high rates of gene flow (McGraw & Antonovics 1983a). Because many arctic species are long-lived with substantial vegetative growth and relatively low rates of successful reproduction via seed (Bliss 1971; McGraw & Fetcher 1992), typical reciprocal transplant experiments that follow individuals for <5 years may be inadequate for quantifying the extent of ecotypic differentiation or characterizing the relative influence of genotype and environment on phenotype. Although local adaptation in long-lived perennials from a range of environments has been studied extensively, reciprocal transplant experiments have generally not been monitored for more than 6 years (but see Miglia et al. 2005; Campbell & Waser 2007; Sonesson et al. 2007; Wright 2007).

Here, we report the results of two 30-year-old reciprocal transplant experiments in Alaskan tundra plants. In the first, Dryas octopetala individuals from three populations growing along a gradient from an exposed fellfield to a more protected snowbed were transplanted to gardens in snowbed, fellfield and intermediate sites near Eagle Summit, Alaska (McGraw & Antonovics 1983a,b). In the second experiment, Eriophorum vaginatum tussocks were reciprocally transplanted to six sites along a broad latitudinal gradient in interior Alaska (Shaver, Fetcher & Chapin 1986). These two experiments, with similar design and history, differed in form and function of plant species, type of environmental gradient and potential for gene flow between populations. D. octopetala is a dwarf shrub (Rosaceae) that dominates arctic fellfields while E. vaginatum is a tussock-forming sedge (Cyperaceae) that dominates mesic arctic tundra. While the distance between farthest D. octopetala gardens was 150 m, the two most distant E. vaginatum gardens were 565 km apart.

In 2010, we revisited each of the reciprocal transplant gardens with two main objectives. First, for both species, we asked whether the cumulative environmental effects on transplants resulted in home site advantage 30 years after the initial transplant. While ecotypic differentiation was previously observed for D. octopetala (McGraw & Antonovics 1983a; McGraw 1987), the magnitude of differentiation may have changed with the cumulative effects of many years in each environment. Alternatively, rapid climate change in the arctic (e.g. Hinzman et al. 2005) may have altered the selection regime over the intervening decades and changed the relative advantage of ecotypes in each environment.

Genetic differentiation in the E. vaginatum populations was established previously (Shaver, Fetcher & Chapin 1986; Fetcher & Shaver 1990), but survival of tussocks was uniformly high for all populations in all sites during 1993; therefore, home site advantage was not documented. We also asked whether differences in plasticity between populations could help explain long-term survival patterns of populations transplanted to foreign sites. McGraw (1987) documented greater morphological plasticity for D. octopetala snowbed ecotypes compared to the fellfield ecotype, which resulted in lower mortality of snowbed ecotypes in the fellfield site after an initial die-off. We asked whether this initial difference in plasticity resulted in greater success of snowbed ecotypes in the long term. Likewise, Fetcher & Shaver (1990) noted greater morphological plasticity in the three E. vaginatum populations from the ‘southern’ (i.e. south of the Brooks Range) sites compared to those from ‘northern’ (i.e. north of the Brooks Range) sites. Because there has been a general trend of increasing global surface air temperatures (Hinzman et al. 2005; Bourne et al. 2010), we hypothesized that plants from southern E. vaginatum populations would have greater success in northern sites than plants from northern populations in southern sites. We asked whether these differences in plasticity had persisted and whether the more plastic populations ultimately showed greater success in foreign sites, or whether there were limits to the effects of morphological adjustments, such that selection acted against foreign genotypes despite an acclimation response. We expected that the plasticity we observed in both species would be adaptive in the long term.

Materials and methods

PLANT SPECIES

Dryas octopetala L. (Rosaceae) is a dwarf shrub species that typically inhabits open, rocky sites and has a broad arctic and alpine distribution. In Alaska, there are two extreme subspecies (D. octopetala ssp. octopetala and D. octopetala ssp. alaskensis) in addition to a broad range of phenotypically intermediate hybrids between the two (Hultén 1959; McGraw & Antonovics 1983a). D. octopetala ssp.
Dryas octopetala has small (5–15 mm long) deciduous leaves and is found along exposed alpine ridges, or fellfields, while D. octopetala ssp. alaskensis has larger (15–50 mm long) evergreen leaves and occurs commonly in more protected sites, or snowbeds. Individuals of both subspecies form prostrate mats of shoots connected by woody stems. Fellfield and snowbed forms can be found growing in close proximity, and hybrid swarms occur in intermediate habitats.

Eriophorum vaginatum L. (Cyperaceae) is a tussock-forming sedge with a circumboreal distribution that is the dominant member of many plant communities in moist arctic tundra. Full-sized adult tussocks can consist of 300–600 live tillers (Fetcher & Shaver 1982). During the course of a growing season, a tiller can produce between one and three daughter tillers, with individual tillers typically living <8 years (Fetcher & Shaver 1983). Tussocks are assumed to comprise vegetative offspring of a single individual and can persist well over 100 years (Mark et al. 1985). Mature tussocks vary widely in size, from up to 50 cm tall in southern populations to 15 cm tall in northern populations, and leaf length ranges from 75 mm in the north to 325 mm in the south (Shaver, Fetcher & Chapin 1986).

**STUDY SITES**

**Dryas octopetala** – In late July, 1979, reciprocal transplant gardens were established along an altitudinal mesotopographic gradient near Eagle Summit Alaska (Fig. 1) where D. octopetala ssp. octopetala occurred on a ridgetop (fellfield) and D. octopetala ssp. alaskensis occurred in a snowbed 50- to 150-m downslope (site described in detail in McGraw & Antonovics 1983a). Intermediate plants were found in a narrow band of vegetation between the two extreme sites.

**Eriophorum vaginatum** – In 1980–82, six reciprocal transplant gardens of E. vaginatum were established along a latitudinal gradient within interior Alaska (Shaver, Fetcher & Chapin 1986). Three sites north of the Brooks Range (TL, Toolik Lake; SAG, Sagwon; and PB, Prudhoe Bay) and three sites south of the Brooks Range (EC, Eagle Creek; NN, No Name Creek; and CF, Coldfoot) were chosen to include a range of elevations and latitudes (Fig. 1). Although there were differences among sites in neighbour species identity and diversity, all six sites were dominated by E. vaginatum.

**EXPERIMENTAL PROCEDURES**

**Dryas octopetala** – At the time the gardens were established, 10 adult plants from each of the three populations were planted into each of the three sites (3 populations × 3 sites × 10 individuals per population per site). For all transplants, individuals were removed with sufficient soil to minimize damage to root systems; thus, some soil was transferred with each plant. These gardens were censused for individual survival at least every other year from 1981 to 1993. In 2009, we revisited the gardens and confirmed the positions of individuals with maps. Specific individuals were positively identified by remnants of wooden lath stakes that remained in place, and where these were absent, by remains of strings from the original tags wrapped around woody stems. We conducted a final census in 2010, recording survival of all plants and counting the number of surviving shoots as well as the number of flowers on those shoots.

**Eriophorum vaginatum** – In each of the six sites, 10 tussocks from each of the other sites were transplanted into holes left by the removal of tussocks at that site. In addition, 10 local tussocks were planted back into each site of origin (total of 6 populations × 6 sites × 10 individuals per population per site). At the time of garden establishment, entire tussocks from each site were cut out of the soil below the moss level using a serrated knife. This method resulted in minimal damage to tussocks because this species has deciduous roots that re-grow each year from the rhizomes of each live tiller within the tussock. Except for CF, which was planted in 1982, all gardens were established in 1980. Because a demographic analysis of tillers from four populations (NN, CF, TL and SAG) in three of the gardens (CF, TL and SAG) revealed an average generation time of 4.75 years (range = 3.62–5.84; J.B. McGraw, J. Chandler & N. Fetcher, unpubl. data), we assumed that at least five generations of vegetative growth have occurred since the initial transplant. Because maternal effects are likely to have disappeared with just two rounds of clonal propagation (Schwaegerle, McIntyre & Swingley 2000) and because seedling recruitment is virtually zero within tussocks (McGraw & Shaver 1982), we considered phenotypic differences among populations detected in 2010 to be a consequence of broad-sense genetic variability.

In 2009, we visited each of the gardens except PB and placed new wooden stakes to mark as many of the 60 original tussocks as possible. We considered all tussocks to be alive if there was at least one surviving tiller. For a haphazardly chosen subsample of tillers (n = 3 in 1983 and

Fig. 1. Map of interior Alaska showing approximate locations of transplant gardens for Dryas octopetala (Eagle Summit) and Eriophorum vaginatum (Eagle Creek, No Name Creek, Coldfoot, Toolik Lake, Sagwon and Prudhoe Bay).

1993; \( n = 12 \) in 2010) on each tussock, we counted the total number of green leaves and measured the length of the two longest leaves. In 2010, there were some tussocks with fewer than 12 tillers, in which case we measured all those alive. In addition to counting the number of green leaves in 2010, we also quantified the level of senescence for every yellowing leaf by categorizing the proportion of yellow as > 25%, > 50% or 100% senesced. Finally in 2010, we measured the diameter of each tussock and counted the number of flowering stems.

**DATA ANALYSIS**

*Dryas octopetala* – We used a nominal logistic model (npar v. 6.0.2; SAS Institute, Inc., Cary, NC, USA) to determine whether the 31-year survival of *D. octopetala* ecotypes depended upon the site into which they were transplanted. Missing data and very low variability in survival for particular ecotypes in particular gardens (i.e. in the nine possible garden \( \times \) ecotype combinations, five had either zero or all individuals surviving) made multiple coefficients in the full factorial model unstable. To improve stability, we coded each of the ecotypes in each garden as either originating from the home site or an away site. Thus, the model included the predictor variables garden (2 d.f.) and origin (1 d.f.), with survival (0 or 1) as the response variable. The interaction term was not estimable due to the complete absence of individuals of foreign ecotypes in the snowbed garden. We used the same model in two separate parametric analyses with number of shoots and number of flowers per shoot as response variables.

*Eriophorum vaginatum* – We used a nominal logistic model to determine whether survival of *E. vaginatum* tussocks depended upon the garden into which they were planted and, in particular, whether survival of tussocks from each population was greatest in their home garden. Due to missing data and very low variability in survival within populations within a garden, it was not possible to analyse a complete factorial design with effects of garden, population and their interaction. Stability of the model was again improved by coding each population as originating from the home site or an away site, as we did in the analysis of survival for *Dryas octopetala*. Thus, the model included garden (5 d.f.), origin (1 d.f.) and their interaction as predictor variables with survival (0 or 1) as the response variable.

We used this same model to determine whether home site advantage was manifested in flower production. Total flower number per tussock included zeroes for those tussocks that had no flowers. To determine whether leaf senescence differs among gardens or populations and whether there is an interaction between garden and population, we used a two-way analysis of variance with garden, population and their interaction as predictor variables. The response variable we compared was the number of leaves per tiller that were 25% or 50% senesced.

We quantified tiller size by multiplying the length of the longest leaf (in mm) by the total number of green leaves (usually 2, 3 or 4). This tiller index is highly correlated with tiller mass (Shaver, Fetcher & Chapin 1986). To determine whether trends observed early in the life of the gardens persisted, we analysed our 1993 and 2010 tiller index data using the same approach used by Fetcher & Shaver (1990) on tiller index data collected in 1983. Population values were calculated as the mean tiller index across all source populations in each garden and hence estimated broad-sense genetic differences. Garden values were calculated as the mean tiller index across all source populations in each garden and represent environmental differences. To make the analyses for 1993 and 2010 comparable, we randomly selected three of the 12 tillers measured in 2010 for inclusion in the calculation of population and garden tiller index values. We compared the plasticity in tiller size among populations by estimating the slopes of the regressions of population value on garden value (Finlay & Wilkinson 1963). Since the mean slope for this relationship is one, we compared the slope for each population to one in each year. Populations with a slope greater than one were considered most plastic, and those with slopes equal to one represent populations that are most dynamically stable (i.e. the adjusted phenotype closely matches the mean for that environment) (Becker & Léon 1988; Lacaze, Hayes & Korol 2009). Because this methodology ignores the sampling variation of the estimates of population-specific means for each garden, as well as the overall mean for each garden, the results of these analyses are intended largely as a means for comparing current trends with those first measured by the same regression analysis immediately following the transplant of the six *E. vaginatum* populations (Fetcher & Shaver 1990).

Fetcher & Shaver (1990) hypothesized that more plastic genotypes from warmer environments may have greater success in new environments created by climate change than those from colder environments with less plasticity. To test this hypothesis, we regressed our measure of plasticity for each population (i.e. the slope of population mean tiller size on garden mean tiller size) against the difference in percentage survival of that population between home and away gardens. If plasticity was adaptive, we would expect that those populations with high plasticity would have a small difference in survival between home and away gardens, whereas populations with low plasticity would experience much-reduced survival in away gardens relative to home gardens (i.e. the slope of the fit between the regression coefficient and the difference in survival between home and away gardens would be negative).

**Results**

**DRYAS OCTOPETALA**

Across all ecotypes, plants in the snowbed garden had significantly lower survival than those in the fellfield or intermediate gardens (Table 1, Fig. 2). Although the overall effect of population origin was statistically significant such that there was greater survival in home sites (Table 1), this was true only in the snowbed and fellfield gardens (Fig. 2). After 31 years in the snowbed garden, only individuals of the snowbed ecotype survived. In the fellfield garden, there was high mortality of the snowbed ecotype between 1979 and 1993, and, by 2010, no individuals of this ecotype survived. The intermediate garden had the highest rates of survival, with all 10 of the snowbed individuals alive after 30 years, as well as five intermediate and six fellfield individuals. A G-test for goodness of fit (Sokal & Rohlf 1981) showed that this difference in survival among populations in the intermediate garden differed from the null expectation that survival of transplants would be independent of the population from which they originated (\( G = 9.329, P = 0.0094 \)).

Home ecotypes did not have higher rates of flowering (i.e. number of flowers per surviving shoot) in 2010 than those transplanted from away sites (Table 1). In fact, in the intermediate garden, where there were survivors of all three ecotypes, a one-way analysis of variance revealed that the number of flowers produced per shoot (\( \overline{X}_{\text{fellfield}} = 0.015; \overline{X}_{\text{intermediate}} = 0.021; \overline{X}_{\text{snowbed}} = 0.020 \)) was not significantly different among ecotypes (\( F = 0.06; P = 0.94 \)). In the fellfield
home site advantage in arctic plants

Table 1. Results of analyses comparing survival, flower number and shoot number of D. octopetala ecotypes in 2010 among fellfield, intermediate and snowbed transplant gardens (across all ecotypes) and among ecotypes planted in gardens at home and away sites.

<table>
<thead>
<tr>
<th>Effect</th>
<th>d.f.</th>
<th>Level</th>
<th>Survival</th>
<th>Number of flowers (per shoot)</th>
<th>Number of shoots</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td>%</td>
<td>Mean F P</td>
<td>Mean F P</td>
</tr>
<tr>
<td>Garden</td>
<td>2</td>
<td>Fellfield</td>
<td>63</td>
<td>0.015 1.67 0.20</td>
<td>110.58 4.36 0.02</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Intermediate</td>
<td>70</td>
<td>0.016</td>
<td>84.65</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Snowbed</td>
<td>27</td>
<td>0.045</td>
<td>8.47</td>
</tr>
<tr>
<td>Origin</td>
<td>1</td>
<td>Home</td>
<td>77</td>
<td>0.031 0.65 0.43</td>
<td>71.57 0.08 0.78</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Away</td>
<td>42</td>
<td>0.020</td>
<td>64.23</td>
</tr>
</tbody>
</table>

In 2010, the proportion of plants flowering was small in all six gardens, ranging from 3% at PB to 21% at EC. There were significant differences among gardens in total flower production with tussocks in the NN garden producing, on average, more than twice as many flowers as the next most prolific garden (Fig. 4). As with survival, tussocks transplanted into their site of origin had higher rates of flowering than those transplanted to foreign sites ($\bar{x}_{\text{Home}} = 1.37, \bar{x}_{\text{Away}} = 0.28$; Table 2). The greatest difference between the mean number of flowers produced by home and away tussocks occurred in the gardens at the lower latitudes (Fig. 4). In fact, there was a 20-fold difference in number of flowers between NN tussocks and tussocks from other sites planted in the NN garden and a six-fold difference between CF tussocks and tussocks from other sites planted in the CF garden.

The number of leaves that had senesced at the time of our censuses in late July was not different among populations ($P = 0.70$), but there was an effect of garden ($P < 0.01$). Across all tussocks, gardens located south of the Brooks Range tended to have more senesced leaves than more northern gardens (Fig. 5). There was not a significant garden × population effect ($P = 0.71$).

Across all populations, final (2010) tiller size decreased with increasing latitude of the garden into which tussocks were transplanted (linear regression, $\beta = -76.35, P < 0.0001$). The maximum mean garden tiller size was greater in 2010 than in 1993, but the pattern of the relationship between population and garden mean tiller size was essentially the same for all six populations in 1993 and 2010 (Fig. 6). For all three of the northern populations, the slopes describing the relationship were significantly $< 1$, while those for southern populations were equal to or greater than one (Table 3). Slopes of one represent dynamically stable populations, where the response of the population is the same as the mean phenotypic response of all populations (Lacaze, Hayes & Korol 2009). Our results from 1993 and 2010 confirm differences in plasticity that were initially observed in the 1983 census (Fetcher & Shaver 1990). These differences, however, did not result in higher 30-year survival of tussocks from the most plastic populations when planted in away sites (Fig. 7).

Discussion

Reciprocal transplant experiments that span decades are rare, but have the potential to reveal evidence for adaptation that is undetectable in shorter experiments, especially for long-lived species with short growing seasons. We found evidence for ecotypic differentiation that became stronger over time in both D. octopetala and E. vaginatum. Survival of fellfield and snowbed individuals of D. octopetala declined in snowbed and

ERIOPHORUM VAGINATUM

Based on the 316 tussocks (of the original 360) that we unequivocally identified, overall survival after 30 years across all gardens was close to 90% for all genotypes except those of the smallest tussocks from the northernmost site (PB; Fig. 3). In 1993, 13 years after the gardens were established, only six of the original 360 tussocks had died (98% survival). In 2010, all but one population (TL) had 100% survival when transplanted back into the site of origin. This home site advantage (96% survival at home and 86% away) is reflected in the highly significant effect of origin in our analysis (Table 2). The strength of home site advantage varied significantly among gardens (Table 2, significant garden × origin interaction; Fig. 3). In particular, survival of tussocks from foreign sites was lowest in NN, CF and SAG gardens (74%, 75% and 78%, respectively) and highest in TL, PB and EC gardens (96%, 95% and 92%, respectively).

In 2010, the proportion of plants flowering was small in all six gardens, ranging from 3% at PB to 21% at EC. There were significant differences among gardens in total flower production with tussocks in the NN garden producing, on average, more than twice as many flowers as the next most prolific garden (Fig. 4). As with survival, tussocks transplanted into...
fellfield gardens, respectively, over 31 years, until each ecotype was eventually completely eliminated in the reciprocal garden. This local extinction of the foreign ecotype in the extreme gardens suggests that selection counteracting gene flow from the foreign environment was even stronger than previously estimated (McGraw & Antonovics 1983a), and explains the spatial separation of extant snowbed and fellfield ecotypes in the face of persistent gene flow. Although mortality of *E. vaginatum* tillers occurred throughout the 30-year experiment, mortality of tussocks was still very low 13 years after transplanting. It was not until our 2010 census that differential mortality of tussocks, which are comprised of hundreds of tillers, provided clear evidence for home site advantage. Further evidence for local adaptation of *E. vaginatum* comes from the greater rates of flower production by tussocks transplanted to their home site compared to those planted into foreign sites. Local adaptation in both species was accompanied by morphological differences among populations that were expressed soon after transplant (McGraw & Antonovics 1983a; Shaver, Fetcher & Chapin 1986). Because no *D. octopetala* snowbed individuals persisted on the fellfield and no fellfield individuals persisted on the snowbed in 2010, we were unable to reassess the genetic differences in morphology between *D. octopetala* ecotypes. The generally high survival across all tussocks in the *E. vaginatum* gardens, however, allowed us to measure vegetative characters in addition to survival and reproduction in those gardens. We found significant plasticity in tiller size in that plants from all populations grown in high latitude gardens tended to be smaller than those grown in gardens at lower latitudes. This result is consistent with previous results from *E. vaginatum* (Shaver, Fetcher & Chapin 1986) as well as other species (e.g. Chapin & Chapin 1981; Li, Suzuki & Hara 1998; Santamaria et al. 2003) and is unlikely to be the result of differential survival of small and large individuals in cool and warm sites given that the pattern we observed parallels that found prior to any tussock mortality (Shaver, Fetcher & Chapin 1986).

Perhaps surprisingly, there was no evidence that differences in timing of senescence in mid-season have evolved in response to differences in the length of the growing season along the latitudinal gradient. Instead, we found that tussocks from all populations responded plasticly to environmental variability, having the least number of senescing leaves in July in the farthest north garden. While lower temperatures are typically associated with earlier senescence in tundra plants (McGraw, Chester & Stuart 1983), our result, based on a single census that occurred prior to the timing of greatest leaf senescence (Shaver & Laundre 1997), may be a function of later initiation of green leaf production at PB and subsequent later senescence. Observations from August of 1983 (Fetcher, pers. obs.) showed that northern tussocks senesced earlier in Coldfoot and Eagle Creek than southern tussocks did, suggesting that genetic differences in senescence may not be evident until later in the season and that these differences could limit the ability of northern tussocks to utilize the extended growing season afforded by a warmer climate.

In addition to genetic differentiation in morphological trait means, prior research in both *D. octopetala* (McGraw & Antonovics 1983a; McGraw 1987) and *E. vaginatum* (Fetcher & Shaver 1990) gardens revealed differences in morphological plasticity among populations. The snowbed *D. octopetala* ecotype and the southern *E. vaginatum* ecotypes were both more plastic than those from fellfield and northern populations, respectively. In addition, the least plastic ecotypes were native

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**Fig. 2.** Survival (%) of three forms of *Dryas octopetala* (ssp. *octopetala*, ssp. *alaskensis* and their intermediate) over 31 years when planted in a reciprocal transplant experiment in (a) fellfield, (b) intermediate and (c) snowbed sites. In each graph, survival of the home ecotype is illustrated as the solid black line with filled circles.
to the least productive environments – fellfield sites had lower nutrient availability and less biomass than snowbed sites (Miller 1982), and productivity was limited by low temperatures in the northern *E. vaginatum* sites (Shaver, Fetcher & Chapin 1986), consistent with the hypothesis that plasticity is favoured in productive sites (Grime 1977; Grime, Crick & Rincón 1986; Chapin 1980, 1988). Because phenotypic plasticity allows populations to rapidly increase mean fitness in new environments (e.g. Hendry et al. 2011), we anticipated that the differences in plasticity would have consequences for the fate of transplanted individuals. For example, most *E. vaginatum*

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**Fig. 3.** Survival of reciprocally transplanted *Eriophorum vaginatum* tussocks from six populations (CF, Coldfoot; NN, No Name Creek; EC, Eagle Creek; TL, Toolik Lake; SAG, Sagwon; and PB, Prudhoe Bay) over 30 years in gardens created at (a) CF, (b) NN, (c) EC, (d) TL, (e) SAG and (f) PB sites. In each graph, survival of the home ecotype is illustrated as the solid black line with filled circles. In many cases, overlapping lines prevent all lines from being observable on graphs.

**Table 2.** Results of analyses comparing survival and flower number of *E. vaginatum* genotypes in each of six gardens created along a latitudinal gradient in interior Alaska.

<table>
<thead>
<tr>
<th>Effect</th>
<th>d.f.</th>
<th>( \chi^2 )</th>
<th>( P )</th>
<th>( F )</th>
<th>( P )</th>
</tr>
</thead>
<tbody>
<tr>
<td>Garden</td>
<td>5</td>
<td>3.33</td>
<td>0.65</td>
<td>8.04</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>Origin</td>
<td>1</td>
<td>8.28</td>
<td>0.004</td>
<td>34.70</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>Garden × Origin</td>
<td>5</td>
<td>11.25</td>
<td>0.047</td>
<td>6.41</td>
<td>&lt;0.0001</td>
</tr>
</tbody>
</table>

mortality in the southern sites appeared to result from burial of northern population tussocks by moss (Fetcher, pers. obs.). A lack of plasticity may have prevented the northern tussocks from producing long leaves and tillers that would have allowed them to escape burial. Overall, however, our results did not support the hypotheses of McGraw (1987) nor Fetcher & Shaver (1990) that the long-term success of transplants into foreign sites would be positively related to plasticity. There are several possible explanations for this lack of a relationship. Genetic or developmental constraints may have prevented ecotypes in foreign sites from adjusting phenology or physiology along with morphology in a functionally appropriate manner (De Witt, Sih & Wilson 1998). In addition, the plasticity we observed may not be positively related to fitness across sites if morphological variability is simply a passive response to resource availability (Alpert & Simms 2002; van Kleunen & Fischer 2005; Ghalambor et al. 2007), or if costs of plasticity outweigh the benefits in at least some environments (e.g. De Witt, Sih & Wilson 1998; Auld, Agrawal & Relyea 2010; Crispo et al. 2010).

From the perspective of 30-year survival within both sets of reciprocal transplant gardens, this study revealed a pattern of strong local adaptation of populations. Upon closer examination, some evidence suggests a northward or upward shift in the optimum environment for each ecotype. For example, both...
the superior survival of snowbed plants of *D. octopetala* in the intermediate garden and the larger shoot populations of intermediate plants in the fellfield garden suggest a subtle upward shift whereby the downslope genotype is performing well in conditions upslope from its site of origin. In the *E. vaginatum* gardens, southern populations transplanted to northern gardens survived at a higher rate than northern populations transplanted south, a pattern that was revealed only since 1993. While the garden environments have likely changed over 30 years in many ways, both of these results would be consistent with a climate shift, which has in fact been observed in the past 30 years (warming of ca. 0.48 °C in Fairbanks, AK to 0.87 °C in Barrow, AK).

The strong local adaptation we found, and that is, in fact, common in arctic species (e.g. Mooney & Billings 1961; Shaver, Chapin & Billings 1979; Chapin & Chapin 1981; Chapin & Oechel 1983; McGraw & Antonovics 1983a; Shaver, Fetcher & Chapin 1986), means that treating either species as a homogenous unit is likely to be inadequate when making predictions about the effects of climate change (Atkins & Travis 2010), even though both *D. octopetala* and *E. vaginatum* have broad arctic distributions. Locally adapted individuals may be unable to tolerate warmer temperatures even if those temperatures are within a species-wide range of tolerable temperatures.

Table 3 Slopes of regressions of population mean tiller index value on garden mean tiller index value for *E. vaginatum* tiller index from six reciprocal transplant gardens in interior Alaska. Values of the *t* statistic, and associated *P* values, test the null hypothesis that *β* = 1, or the mean slope.

<table>
<thead>
<tr>
<th>Year</th>
<th>Slope, β</th>
<th><em>t</em></th>
<th><em>P</em></th>
<th>Slope, β</th>
<th><em>t</em></th>
<th><em>P</em></th>
</tr>
</thead>
<tbody>
<tr>
<td>1993</td>
<td>1.91</td>
<td>5.69</td>
<td>0.002</td>
<td>1.34</td>
<td>3.06</td>
<td>0.028</td>
</tr>
<tr>
<td></td>
<td>1.52</td>
<td>2.73</td>
<td>0.041</td>
<td>1.16</td>
<td>1.29</td>
<td>0.254</td>
</tr>
<tr>
<td></td>
<td>1.19</td>
<td>0.78</td>
<td>0.471</td>
<td>1.23*</td>
<td>1.59</td>
<td>0.273</td>
</tr>
<tr>
<td></td>
<td>0.60</td>
<td>−2.54</td>
<td>0.052</td>
<td>0.68</td>
<td>−3.44</td>
<td>0.018</td>
</tr>
<tr>
<td></td>
<td>0.22</td>
<td>−4.85</td>
<td>0.005</td>
<td>0.51</td>
<td>−4.95</td>
<td>0.004</td>
</tr>
<tr>
<td></td>
<td>0.30</td>
<td>−4.96</td>
<td>0.004</td>
<td>0.50</td>
<td>−5.82</td>
<td>0.002</td>
</tr>
</tbody>
</table>

*CF was the only population for which there was also a significant (*P* < 0.0001) quadratic component to the relationship between population and garden tiller index values.

Fig. 7. Difference in the proportional survival between tussocks of *Eriophorum vaginatum* planted in home and away gardens regressed against the mean plasticity of tussocks from each population (CF, Coldfoot; NN, No Name Creek; EC, Eagle Creek; TL, Toolik Lake; SAG, Sagwon; and PB, Prudhoe Bay) where plasticity was measured as the slope of the line relating genotypic and environmental values for tiller index.

(e.g. Souther & McGraw 2011). While the long-lived genets of both *D. octopetala* and *E. vaginatum* may persist in a new environment to which they are poorly adapted, individual longevity and low rates of seedling establishment reduce the ability of new genotypes, from populations adapted to warmer environments, to invade, resulting in a temporal lag in adaptive response (Jump & Penuelas 2005; Aitken et al. 2008). The ultimate success of genotypes that invade sites at higher latitude may also be constrained by the fact that, while adapted to the mean temperature into which they have migrated, they may not respond appropriately to other important environmental components such as photoperiod (Visscher 2008). Additional long-term studies that quantify genetic and plastic responses to selection in a warming climate are needed to improve our understanding of the role of microevolutionary processes in the response of plant communities to climate change (Gienapp et al. 2008; Halon & Strauss 2008).

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**References**


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