

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23

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

Cynthia C. Bennington^{1*}, Ned Fetcher², Milan C. Vavrek³, Gaius R. Shaver⁴, Kelli Cummings² and James B. McGraw⁵

¹Department of Biology, Stetson University, 421 N Woodland Blvd Unit 8264, DeLand, FL 32723, U.S.A.

²Institute for Environmental Science and Sustainability, Wilkes University, Wilkes-Barre, PA 18766

³Department of Land Resources, Glenville State University, 200 High Street, Glenville, WV 26351

⁴The Ecosystems Center, Marine Biological Laboratory, Woods Hole, MA 02543

24 ⁵Department of Biology, West Virginia University, P.O. Box 6057, Morgantown, WV 26506-
25 6057, U.S.A.

26 Running head: Home site advantage in arctic plants

27 **Summary**

28

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

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

45 3. For *D. octopetala*, the original patterns of local adaptation observed in the decade
46 following transplant appeared even stronger after three decades, with the complete

47 elimination of foreign ecotypes in both fellfield and snowbed environments. For *E.*
48 *vaginatum*, differential survival of populations was not evident 13 years after
49 transplant, but was clearly evident 17 years later. There was no evidence that
50 plasticity was associated with increased survival of foreign populations in novel
51 sites for either *D. octopetala* or *E. vaginatum*.

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

56

57 **Key-words:** adaptation; *Dryas octopetala*; Ecological genetics and ecogenomics,
58 *Eriophorum vaginatum*; genetic differentiation; phenotypic plasticity; tussock tundra

59

60 **Introduction**

61

62 Genetic differentiation among plant populations in response to selection on
63 morphological, phenological and physiological characters has resulted in locally adapted
64 genotypes, or ecotypes, across narrow to broad spatial scales. Ecotypes may form over
65 short distances in response to edaphic characteristics (e.g. Bennington & McGraw 1995;
66 Brady *et al.* 2005; Knight *et al.* 2006; Sambatti & Rice 2006; Wright 2007; Hufford *et al.*
67 2008), biotic interactions (e.g. Liancourt & Tielborger 2009), or topographic features (e.g.
68 Byars *et al.* 2007; Gonzalo-Turpin & Hazard 2009), while multiple factors, including
69 climate, may result in such differentiation on larger scales (e.g. Chapin & Chapin 1981; Joshi
70 *et al.* 2001; Rutter & Fenster 2007). While ecotypic specialization confers a fitness
71 advantage relative to other genotypes in the local environment, maladaptation of foreign
72 genotypes could inhibit their invasion into new environments (Hereford 2009). Genotypes
73 that exhibit phenotypic plasticity, and hence have an extensive niche breadth, may have
74 greatest success in novel environments (Bradshaw 1965; van Valen 1965; Sultan & Spencer
75 2002; Richards *et al.* 2006). Although phenotypic plasticity and genetic differentiation
76 have been described as alternate solutions for coping with environmental variability
77 (Schlichting 1986; Levin 1988), there is growing evidence that phenotypic plasticity may
78 facilitate genetic differentiation in response to environmental variability (e.g. Schlichting
79 2004; West-Eberhard 2005; Pigliucci 2007; Pfenning *et al.* 2010). This is true if plastic
80 responses increase survival of genotypes across environments, and expose individuals to
81 natural selection that favours a genetic response in the same direction as the phenotypic

82 one (e.g. Crispo 2007). Thus, predictions about the ability of populations to expand their
83 range or cope with environmental change depend upon an estimation of the degree of both
84 genetic differentiation and phenotypic plasticity (e.g. Nicotra *et al.* 2010; Hendry *et al.*
85 2011).

86 Reciprocal transplant experiments have been used extensively to quantify the relative
87 magnitude of environmental and genetic influences on plant phenotype (Primack & Kang
88 1989; Linhart & Grant 1996). In arctic and alpine systems, reciprocal transplant
89 experiments conducted over exposure and/or elevational gradients (e.g. Clausen *et al.*
90 1940, 1948; McGraw & Antonovics 1983a, b; Galen *et al.* 1991; Shimono *et al.* 2009) as well
91 as latitudinal gradients (e.g. Chapin & Chapin 1981, Shaver *et al.* 1986, Fetcher & Shaver
92 1990) have demonstrated genetic differentiation in morphological and physiological traits.
93 In some cases, clear evidence for local adaptation has been found even in the face of
94 potentially high rates of gene flow (McGraw & Antonovics 1983a). Because many arctic
95 species are long-lived with substantial vegetative growth and relatively low rates of
96 successful reproduction *via* seed (Bliss 1971, McGraw & Fetcher 1992), typical reciprocal
97 transplant experiments that follow individuals for less than five years may be inadequate
98 for quantifying the extent of ecotypic differentiation or characterizing the relative influence
99 of genotype and environment on phenotype. Although local adaptation in long-lived
100 perennials from a range of environments has been studied extensively, reciprocal
101 transplant experiments have generally not been monitored for more than six years (but see
102 Miglia *et al.* 2005; Campbell & Waser 2007; Sonesson *et al.* 2007; Wright 2007).

103 Here, we report the results of two 30-year-old reciprocal transplant experiments in
104 Alaskan tundra plants. In the first, *Dryas octopetala* individuals from three populations

105 growing along a gradient from an exposed fellfield to a more protected snowbed were
106 transplanted to gardens in snowbed, fellfield, and intermediate sites near Eagle Summit,
107 Alaska (McGraw & Antonovics 1983a, b). In the second experiment, *Eriophorum vaginatum*
108 tussocks were reciprocally transplanted to six sites along a broad latitudinal gradient in
109 interior Alaska (Shaver *et al.* 1986). These two experiments, with similar design and
110 history, differed in form and function of plant species, type of environmental gradient, and
111 potential for gene flow between populations. *D. octopetala* is a dwarf shrub (Rosaceae) that
112 dominates arctic fellfields while *E. vaginatum* is a tussock-forming sedge (Cyperaceae) that
113 dominates mesic arctic tundra. While the distance between farthest *D. octopetala* gardens
114 was 150 m, the two most distant *E. vaginatum* gardens were 565 km apart.

115 In 2010, we revisited each of the reciprocal transplant gardens with two main
116 objectives. First, for both species, we asked whether the cumulative environmental effects
117 on transplants resulted in home site advantage 30 years after the initial transplant. While
118 ecotypic differentiation was previously observed for *D. octopetala* (McGraw & Antonovics
119 1983a; McGraw 1987), the magnitude of differentiation may have changed with the
120 cumulative effects of many years in each environment. Alternatively, rapid climate change
121 in the arctic (e.g. Hinzman *et al.* 2005) may have altered the selection regime over the
122 intervening decades and changed the relative advantage of ecotypes in each environment.

123 Genetic differentiation in the *E. vaginatum* populations was established previously
124 (Shaver *et al.* 1986, Fetcher and Shaver 1990), but survival of tussocks was uniformly high
125 for all populations in all sites during 1993, therefore, home site advantage was not
126 documented. We also asked whether differences in plasticity between populations could
127 help explain long-term survival patterns of populations transplanted to foreign sites.

128 McGraw (1987) documented greater morphological plasticity for *D. octopetala* snowbed
129 ecotypes compared to the fellfield ecotype, which resulted in lower mortality of snowbed
130 ecotypes in the fellfield site after an initial die-off. We asked whether this initial difference
131 in plasticity resulted in greater success of snowbed ecotypes in the long-term. Likewise,
132 Fetcher and Shaver (1990) noted greater morphological plasticity in the three *E. vaginatum*
133 populations from the “southern” (i.e. south of the Brooks Range) sites compared to those
134 from “northern” (i.e. north of the Brooks Range) sites. Because there has been a general
135 trend of increasing global surface air temperatures (Hinzman *et al.* 2005; Bourne *et al.*
136 2010), we hypothesized that plants from southern *E. vaginatum* populations would have
137 greater success in northern sites than plants from northern populations in southern sites.
138 We asked whether these differences in plasticity had persisted and whether the more
139 plastic populations ultimately showed greater success in foreign sites, or whether there
140 were limits to the effects of morphological adjustments, such that selection acted against
141 foreign genotypes despite an acclimation response. We expected that the plasticity we
142 observed in both species would be adaptive in the long-term.

143

144

145 **Materials and methods**

146

147 **PLANT SPECIES**

148

149 *Dryas octopetala* L. (Rosaceae) is a dwarf shrub species that typically inhabits open,
150 rocky sites and has a broad arctic and alpine distribution. In Alaska, there are two extreme

151 subspecies (*D. octopetala ssp. octopetala* and *D. octopetala ssp. alaskensis*) in addition to a
152 broad range of phenotypically intermediate hybrids between the two (Hultén 1959;
153 McGraw & Antonovics 1983a). *D. octopetala ssp. octopetala* has small (5–15 mm long)
154 deciduous leaves and is found along exposed alpine ridges, or fellfields, while *D. octopetala*
155 *ssp. alaskensis* has larger (15–50 mm long) evergreen leaves and occurs commonly in more
156 protected sites, or snowbeds. Individuals of both subspecies form prostrate mats of shoots
157 connected by woody stems. Fellfield and snowbed forms can be found growing in close
158 proximity, and hybrid swarms occur in intermediate habitats.

159 *Eriophorum vaginatum* L. (Cyperaceae) is a tussock-forming sedge with a circumboreal
160 distribution that is the dominant member of many plant communities in moist arctic
161 tundra. Full-sized adult tussocks can consist of 300–600 live tillers (Fetcher & Shaver
162 1982). During the course of a growing season, a tiller can produce between one and three
163 daughter tillers, with individual tillers typically living less than eight years (Fetcher &
164 Shaver 1983). Tussocks are assumed to comprise vegetative offspring of a single individual
165 and can persist well over 100 years (Mark *et al.* 1985). Mature tussocks vary widely in size,
166 from up to 50 cm tall in southern populations to 15 cm tall in northern populations, and
167 leaf length ranges from 75 mm in the north to 325 mm in the south (Shaver *et al.* 1986).

168

169 STUDY SITES

170

171 *D. octopetala* – In late July, 1979, reciprocal transplant gardens were established along an
172 altitudinal mesotopographic gradient near Eagle Summit Alaska (Fig. 1) where *D.*
173 *octopetala ssp. octopetala* occurred on a ridgetop (fellfield) and *D. octopetala ssp. alaskensis*

174 occurred in a snowbed 50–150m downslope (site described in detail in McGraw &
175 Antonovics 1983a). Intermediate plants were found in a narrow band of vegetation
176 between the two extreme sites.

177
178 *E. vaginatum* – In 1980–82, six reciprocal transplant gardens of *E. vaginatum* were
179 established along a latitudinal gradient within interior Alaska (Shaver *et al.* 1986). Three
180 sites north of the Brooks Range (Toolik Lake - TL, Sagwon - SAG, and Prudhoe Bay- PB) and
181 three sites south of the Brooks Range (Eagle Creek - EC, No Name Creek - NN, and Coldfoot -
182 CF) were chosen to include a range of elevations and latitudes (Fig. 1). Although there
183 were differences among sites in neighbour species identity and diversity, all six sites were
184 dominated by *E. vaginatum*.

185

186 EXPERIMENTAL PROCEDURES

187

188 *D. octopetala* – At the time the gardens were established, ten adult plants from each of the
189 three populations were planted into each of the three sites (3 populations x 3 sites x 10
190 individuals per population per site). For all transplants, individuals were removed with
191 sufficient soil to minimize damage to root systems; thus some soil was transferred with
192 each plant. These gardens were censused for individual survival at least every other year
193 from 1981 to 1993. In 2009, we revisited the gardens and confirmed the positions of
194 individuals with maps. Specific individuals were positively identified by remnants of
195 wooden lath stakes that remained in place, and where these were absent, by remains of
196 strings from the original tags wrapped around woody stems. We conducted a final census

197 in 2010, recording survival of all plants, and counting the number of surviving shoots as
198 well as the number of flowers on those shoots.

199

200 *E. vaginatum* - In each of the six sites, ten tussocks from each of the other sites were
201 transplanted into holes left by the removal of tussocks at that site. In addition, ten local
202 tussocks were planted back into each site of origin (total of 6 populations x 6 sites x 10
203 individuals per population per site). At the time of garden establishment, entire tussocks
204 from each site were cut out of the soil below the moss level using a serrated knife. This
205 method resulted in minimal damage to tussocks because this species has deciduous roots
206 that re-grow each year from the rhizomes of each live tiller within the tussock. Except for
207 CF, which was planted in 1982, all gardens were established in 1980. Because a
208 demographic analysis of tillers from four populations (NN, CF, TL, and SAG) in three of the
209 gardens (CF, TL, and SAG) revealed an average generation time of 4.75 years (range = 3.62–
210 5.84; unpublished data), we assumed that at least five generations of vegetative growth
211 have occurred since the initial transplant. Because maternal effects are likely to have
212 disappeared with just two rounds of clonal propagation (Schwaegerle *et al.* 2000) and
213 because seedling recruitment is virtually zero within tussocks (McGraw & Shaver 1982),
214 we considered phenotypic differences among populations detected in 2010 to be a
215 consequence of broad-sense genetic variability. In 2009 we visited each of the gardens
216 except PB and placed new wooden stakes to mark as many of the 60 original tussocks as we
217 could find. With visits to all six gardens in 2010, we were able to unequivocally locate 88%
218 (n=316) of all (n=360) tussocks. Our success at determining which tussocks were part of
219 the original experiment varied considerably between sites. For the population at No Name

220 Creek, we were only able to find 60% of the previously-marked tussocks because a wildfire
221 occurred at the site in 2004 and the tussocks were large, making old stakes difficult to see.
222 At Sagwon, all tussocks were found.

223

224 All gardens were censused in 1983, 1993 and 2010. At each census, tussocks were counted
225 as alive if there was at least one surviving tiller. For a haphazardly chosen subsample of
226 tillers (n = 3 in 1983 and 1993; n = 12 in 2010) on each tussock, we counted the total
227 number of green leaves and measured the length of the two longest leaves. In 2010, there
228 were some tussocks with fewer than 12 tillers, in which case we measured all those alive.
229 In addition to counting the number of green leaves in 2010, we also quantified the level of
230 senescence for every yellowing leaf by categorizing the proportion of yellow as > 25%, > 50% or
231 100% senesced. Finally in 2010, we measured the diameter of each tussock and counted the
232 number of flowering stems.

233

234 DATA ANALYSIS

235

236 *D. octopetala* – We used a nominal logistic model (JMP v. 6.0.2, SAS Institute, Inc) to
237 determine whether the 31-year survival of *D. octopetala* ecotypes depended upon the site
238 into which they were transplanted. Missing data and very low variability in survival for
239 particular ecotypes in particular gardens (i.e. in the nine possible Garden x Ecotype
240 combinations, five had either zero or all individuals surviving) made multiple coefficients
241 in the full factorial model unstable. To improve stability, we coded each of the ecotypes in
242 each garden as either originating from the Home site or an Away site. Thus, the model

243 included the predictor variables Garden (2 d.f.) and Origin (1 d.f.), with survival (0 or 1) as
244 the response variable. The interaction term was not estimable due to the complete absence
245 of individuals of foreign ecotypes in the snowbed garden. We used the same model in two
246 separate parametric analyses with number of shoots and number of flowers per shoot as
247 response variables.

248

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

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

265 We quantified tiller size by multiplying the length of the longest leaf (in mm) by the
266 total number of green leaves (usually 2, 3 or 4). This tiller index is highly correlated with
267 tiller mass (Shaver *et al.* 1986). To determine whether trends observed early in the life of
268 the gardens persisted, we analyzed our 1993 and 2010 tiller index data using the same
269 approach used by Fetcher and Shaver (1990) on tiller index data collected in 1983.
270 Population values were calculated as the mean tiller index for each population in each
271 garden and hence estimated broad sense genetic differences. Garden values were
272 calculated as the mean tiller index across all source populations in each garden and
273 represent environmental differences. To make the analyses for 1993 and 2010
274 comparable, we randomly selected three of the 12 tillers measured in 2010 for inclusion in
275 the calculation of population and garden tiller index values. We compared the plasticity in
276 tiller size among populations by estimating the slopes of the regressions of population
277 value on garden value (Finlay & Wilkinson 1963). Since the mean slope for this
278 relationship is one, we compared the slope for each population to one in each year.
279 Populations with a slope greater than one were considered most plastic, and those with
280 slopes equal to one represent populations that are most dynamically stable (i.e. the
281 adjusted phenotype closely matches the mean for that environment) (Becker and Léon
282 1988; Lacaze *et al.* 2009). Because this methodology ignores the sampling variation of the
283 estimates of population-specific means for each garden, as well as the overall mean for
284 each garden, the results of these analyses are intended largely as a means for comparing
285 current trends with those first measured by the same regression analysis immediately
286 following the transplant of the six *E. vaginatum* populations (Fetcher and Shaver 1990).

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

298

299 **Results**

300

301 *Dryas octopetala*

302

303 Across all ecotypes, plants in the snowbed garden had significantly lower survival than
304 those in the fellfield or intermediate gardens (Table 1, Fig. 2). Although the overall effect
305 of population origin was statistically significant such that there was greater survival in
306 home sites (Table 1), this was true only in the snowbed and fellfield gardens (Fig. 2). After
307 31 years in the snowbed garden, only individuals of the snowbed ecotype survived. In the
308 fellfield garden, there was high mortality of the snowbed ecotype between 1979 and 1993,
309 and, by 2010, no individuals of this ecotype survived. The intermediate garden had the

310 highest rates of survival, with all 10 of the snowbed individuals alive after 30 years, as well
 311 as five intermediate and six fellfield individuals. A G-test for goodness of fit (Sokal and
 312 Rohlf 1981) showed that this difference in survival among populations in the intermediate
 313 garden differed from the null expectation that survival of transplants would be
 314 independent of the population from which they originated ($G = 9.329$, $P = 0.0094$).

315 Home ecotypes did not have higher rates of flowering (i.e. number of flowers per
 316 surviving shoot) in 2010 than those transplanted from Away sites (Table 1). In fact, in the
 317 intermediate garden, where there were survivors of all three ecotypes, a one-way analysis
 318 of variance revealed that the number of flowers produced per shoot ($\bar{x}_{\text{fellfield}} = 0.015$; $\bar{x}_{\text{intermediate}} = 0.021$; $\bar{x}_{\text{snowbed}} = 0.020$) was not significantly different among
 319 ecotypes ($F = 0.06$; $P = 0.94$). In the fellfield garden, plants of the intermediate ecotype
 320 produced approximately five times more flowers per shoot than fellfield plants
 321 ($\bar{x}_{\text{fellfield}} = 0.005$; $\bar{x}_{\text{intermediate}} = 0.026$) and, in a separate t-test, this difference was significant (t_1
 322 $= 4.90$, $P = 0.05$).

324 There were large differences in the number of shoots per plant among gardens (Table
 325 1). In particular, the few remaining plants in the snowbed garden had very few shoots,
 326 while those in the intermediate and fellfield gardens were much larger. A multiple
 327 comparison test (Tukey HSD) revealed that the difference in shoot number between
 328 fellfield and snowbed gardens was statistically significant, and that shoot number in the
 329 intermediate garden was not different from either fellfield or snowbed. Across gardens, for
 330 plants that remained after 31 years, individuals from home sites did not have more shoots
 331 than those from away sites (Table 1). Because there were no snowbed survivors in the
 332 fellfield and no fellfield survivors on the snowbed, we were unable to measure

333 morphological plasticity across the environmental gradient as was done immediately after
 334 transplant (McGraw & Antonovics 1983a).

335

336 *Eriophorum vaginatum*

337

338 Based on the 316 tussocks (of the original 360) that we unequivocally identified, overall
 339 survival after 30 y across all gardens was close to 90% for all genotypes except those of the
 340 smallest tussocks from the northernmost site (PB; Fig. 3). In 1993, 13 years after the
 341 gardens were established, only six of the original 360 tussocks had died (98% survival). In
 342 2010, all but one population (TL) had 100% survival when transplanted back into the site
 343 of origin. This home site advantage (96% survival at Home and 86% Away) is reflected in
 344 the highly significant effect of Origin in our analysis (Table 2). The strength of home site
 345 advantage varied significantly among gardens (Table 2, significant Garden x Origin
 346 interaction; Fig. 3). In particular, survival of tussocks from foreign sites was lowest in NN,
 347 CF, and SAG gardens (74%, 75%, and 78% respectively) and highest in TL, PB, and EC
 348 gardens (96%, 95%, and 92% respectively).

349 In 2010, the proportion of plants flowering was small in all six gardens, ranging from
 350 3% at PB to 21% at EC. There were significant differences among gardens in total flower
 351 production with tussocks in the NN garden producing, on average, more than twice as
 352 many flowers as the next most prolific garden (Fig. 4). As with survival, tussocks
 353 transplanted into their site of origin had higher rates of flowering than those transplanted
 354 to foreign sites ($\bar{x}_{\text{Home}} = 1.37; \bar{x}_{\text{Away}} = 0.28$; Table 2). The greatest difference between the
 355 mean number of flowers produced by Home and Away tussocks occurred in the gardens at

356 the lower latitudes (Fig. 4). In fact, there was a 20-fold difference in number of flowers
357 between NN tussocks and tussocks from other sites planted in the NN garden and a six-fold
358 difference between CF tussocks and tussocks from other sites planted in the CF garden.

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

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

376

377 **Discussion**

378

379 Reciprocal transplant experiments that span decades are rare, but have the potential to
380 reveal evidence for adaptation that is undetectable in shorter experiments, especially for
381 long-lived species with short growing seasons. We found evidence for ecotypic
382 differentiation that became stronger over time in both *D. octopetala* and *E. vaginatum*.
383 Survival of fellfield and snowbed individuals of *D. octopetala* declined in snowbed and
384 fellfield gardens, respectively, over 31 years, until each ecotype was eventually completely
385 eliminated in the reciprocal garden. This local extinction of the foreign ecotypes in the
386 extreme gardens suggests that selection counteracting gene flow from the foreign
387 environment was even stronger than previously estimated (McGraw & Antonovics 1983a),
388 and explains the spatial separation of extant snowbed and fellfield ecotypes in the face of
389 persistent gene flow. Although mortality of *E. vaginatum* tillers occurred throughout the 30
390 year experiment, mortality of tussocks was still very low 13 years after transplanting. It
391 was not until our 2010 census that differential mortality of tussocks, which are comprised
392 of hundreds of tillers, provided clear evidence for home-site advantage. Further evidence
393 for local adaptation of *E. vaginatum* comes from the greater rates of flower production by
394 tussocks transplanted to their home site compared to those planted into foreign sites.

395 Local adaptation in both species was accompanied by morphological differences among
396 populations that were expressed soon after transplant (McGraw & Antonovics 1983a;
397 Shaver *et al.* 1986). Because no *D. octopetala* snowbed individuals persisted on the fellfield
398 and no fellfield individuals persisted on the snowbed in 2010, we were unable to reassess
399 the genetic differences in morphology between *D. octopetala* ecotypes. The generally high
400 survival across all tussocks in the *E. vaginatum* gardens, however, allowed us to measure
401 vegetative characters in addition to survival and reproduction in those gardens. We found

402 significant plasticity in tiller size in that plants from all populations grown in high latitude
403 gardens tended to be smaller than those grown in gardens at lower latitudes. This result is
404 consistent with previous results from *E. vaginatum* (Shaver *et al.* 1986) as well as other
405 species (e.g. Chapin & Chapin 1981; Li *et al.* 1998; Santamaria *et al.* 2003) and is unlikely to
406 be the result of differential survival of small and large individuals in cool and warm sites
407 given that the pattern we observed parallels that found prior to any tussock mortality
408 (Shaver *et al.* 1986).

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

422 In addition to genetic differentiation in morphological trait means, prior research in
423 both *D. octopetala* (McGraw & Antonovics 1983a; McGraw 1987) and *E. vaginatum* (Fetcher
424 & Shaver 1990) gardens revealed differences in morphological plasticity among

425 populations. The snowbed *D. octopetala* ecotype and the southern *E. vaginatum* ecotypes
426 were both more plastic than those from fellfield and northern populations, respectively. In
427 addition, the least plastic ecotypes were native to the least productive environments -
428 fellfield sites had lower nutrient availability and less biomass than snowbed sites (Miller
429 1982), and productivity was limited by low temperatures in the northern *E. vaginatum*
430 sites (Shaver *et al.* 1986), consistent with the hypothesis that plasticity is favoured in
431 productive sites (Grime 1977; Grime *et al.* 1986; Chapin 1980, 1988). Because phenotypic
432 plasticity allows populations to rapidly increase mean fitness in new environments (e.g.
433 Hendry *et al.* 2011), we anticipated that the differences in plasticity would have
434 consequences for the fate of transplanted individuals. For example, most *E. vaginatum*
435 mortality in the southern sites appeared to result from burial of northern population
436 tussocks by moss (Fetcher, pers. obs.). A lack of plasticity may have prevented the
437 northern tussocks from producing long leaves and tillers that would have allowed them to
438 escape burial. Overall, however, our results did not support the hypotheses of McGraw
439 (1987) nor Fletcher & Shaver (1990) that the long-term success of transplants into foreign
440 sites would be positively related to plasticity. There are several possible explanations for
441 this lack of a relationship. Genetic or developmental constraints may have prevented
442 ecotypes in foreign sites from adjusting phenology or physiology along with morphology in
443 a functionally appropriate manner (deWitt *et al.* 1998). In addition, the plasticity we
444 observed may not be positively related to fitness across sites if morphological variability is
445 simply a passive response to resource availability (Alpert & Simms 2002; van Kleunen &
446 Fischer 2005; Ghalambor *et al.* 2007), or if costs of plasticity outweigh the benefits in at
447 least some environments (e.g. DeWitt 1998; Auld *et al.* 2010; Crispo *et al.* 2010).

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

461 In the future, rising temperatures (IPCC 2007) are generally predicted to lead to
462 increased primary productivity and decreased abiotic stress (Parmesan 2006). In the
463 arctic, tundra shrubs are expected to increase in dominance (Chapin *et al.* 1995; Sturm *et al.*
464 *al.* 2001, Tape *et al.* 2006) and tundra plants are expected to grow taller (Walker *et al.*
465 2006; Hudson & Henry 2009). Plant populations can respond to these changes with: a)
466 shifts in distribution through migration, b) the evolution of traits under selection, or c)
467 both migration and evolution (Holt 1990; Davis & Shaw 2001). Both *D. octopetala* and *E.*
468 *vaginatum* have seeds adapted for long-distance wind dispersal and, especially for *E.*
469 *vaginatum*, increased fire frequency in interior Alaska (e.g. Hu *et al.* 2010) may lead to
470 disturbance that increases chances for migrants to establish. The potential for migration to

471 result in range shifts, however, is limited by the longevity of individual plants and the
472 typically low rates of seedling establishment for both species.

473 The strong local adaptation we found, and that is, in fact, common in arctic species (e.g.
474 Mooney & Billings 1961; Shaver *et al.* 1979; Chapin & Chapin 1981, Chapin & Oechel 1983;
475 McGraw & Antonovics 1983a; Shaver *et al.* 1986), means that treating either species as a
476 homogenous unit is likely to be inadequate when making predictions about the effects of
477 climate change (Atkins & Travis 2010), even though both *D. octopetala* and *E. vaginatum*
478 have broad arctic distributions. Locally adapted individuals may be unable to tolerate
479 warmer temperatures even if those temperatures are within a species-wide range of
480 tolerable temperatures (e.g. Souther & McGraw 2011). While the long-lived genets of both
481 *D. octopetala* and *E. vaginatum* may persist in a new environment to which they are poorly
482 adapted, individual longevity and low rates of seedling establishment reduce the ability of
483 new genotypes, from populations adapted to warmer environments, to invade, resulting in
484 a temporal lag in adaptive response (Jump & Penuelas 2005; Aitken *et al.* 2008; Thuiller *et*
485 *al.* 2008). The ultimate success of genotypes that invade sites at higher latitude may also
486 be constrained by the fact that, while adapted to the mean temperature into which they
487 have migrated, they may not respond appropriately to other important environmental
488 components such as photoperiod (Visser 2008). Additional long-term studies that quantify
489 genetic and plastic responses to selection in a warming climate are needed to improve our
490 understanding of the role of microevolutionary processes in the response of plant
491 communities to climate change (Gienapp *et al.* 2008; Haloin and Strauss 2008).

492

493 **Acknowledgments**

494

495 We would like to thank Zach Fowler, Caitlin Peterson, Melissa Shockey, and Sara Souther
496 for field assistance and Ruth Shaw and two anonymous reviewers for helpful comments to
497 earlier drafts of the manuscript. We would also like to thank Bill Streever and the staff of
498 BP Exploration Alaska for assisting with access to the Prudhoe Bay garden and the Toolik
499 Lake Field Station and the Arctic LTER project (NSF-DEB-1026843) for logistical support.
500 Jason Stuckey, at Toolik Lake Field Station, provided the map in Figure 1. Funding for this
501 research was provided by National Science Foundation grant ARC-0908936 with additional
502 support from NSF-BSR-9024188.

503

504 **References**

505

506 Aitken, S.N., Yeaman, S., Holliday, J.A., Wang, T. & Curtis-McLane, S. (2008) Adaptation,
507 migration or extirpation: climate change outcomes for tree populations. *Evolutionary*
508 *Applications*, **1**, 95-111.

509

510 Alpert, P. & Simms, E.L. (2002) The relative advantages of plasticity and fixity in different
511 environments: when is it good for a plant to adjust? *Evolutionary Ecology*, **16**, 285-297.

512

513 Atkins, K.E. & Travis, J.M.J. (2010) Local adaptation and the evolution of species' ranges
514 under climate change. *Journal of Theoretical Biology*, **266**, 449-457.

515

516 Auld, J.R., Agrawal, A.A. & Relyea, R.A. (2010) Re-evaluating the costs and limits of adaptive

- 517 phenotypic plasticity. *Proceedings of the Royal Society Biological Sciences*, **277**, 503-511.
- 518
- 519 Becker, H.C. & Léon, J. (1988) Stability analysis in plant breeding. *Plant Breeding*, 101, 1-23.
- 520
- 521 Bennington, C.C. & McGraw, J.B. (1995) Natural selection and ecotypic differentiation in
- 522 *Impatiens pallida*. *Ecological Monographs*, **65**, 303-324.
- 523
- 524 Bliss, L.C. (1971) Arctic and alpine plant life cycles. *Annual Review of Ecology and*
- 525 *Systematics*, **2**, 405-438.
- 526
- 527 Bourne, S.M., Bhatt, U.S., Zhang, J. & Thoman, R. (2010) Surface-based temperature
- 528 inversions in Alaska from a climate perspective. *Atmospheric Research*, **95**, 353-366.
- 529
- 530 Bradshaw, A.D. (1965) Evolutionary significance of phenotypic plasticity in plants.
- 531 *Advances in Genetics*, **13**, 115-155.
- 532
- 533 Brady, K.U., Kruckeberg, A.R. & Bradshaw, H.D. (2005) Evolutionary ecology of plant
- 534 adaptation to serpentine soils. *Annual Review of Ecology, Evolution, and Systematics*, **36**,
- 535 243-266.
- 536
- 537 Byars, S.G., Papst, W. & Hoffmann, A.A. (2007) Local adaptation and cogradient selection in
- 538 the alpine plant, *Poa hiemata*, along a narrow altitudinal gradient. *Evolution*, **61**, 2925–
- 539 2941.

540

541 Campbell, D.R. & Waser, N.M. (2007) Evolutionary dynamics of an *Ipomopsis* hybrid zone:
542 Confronting models with lifetime fitness data. *The American Naturalist*, **169**, 298-310.

543

544 Chapin, F.S. III (1980) The mineral nutrition of wild plants. *Annual Review of Ecology and*
545 *Systematics*, **11**, 233-260.

546

547 Chapin, F.S. III & Chapin, M.C. (1981) Ecotypic differentiation of growth processes in *Carex*
548 *aquatilis* along latitudinal and local gradients. *Ecology*, **62**, 1000-1009.

549

550 Chapin, F.S. III & Oechel, W.C. (1983) Photosynthesis, respiration and phosphate absorption
551 by *Carex aquatilis* ecotypes along latitudinal and local environmental gradients. *Ecology*,
552 **64**, 743-751.

553

554 Chapin F.S. III (1988) Ecological aspects of plant mineral nutrition. *Advances in Plant*
555 *Nutrition*, **3**, 161-191.

556

557 Chapin, F.S. III, Shaver, G.R., Giblin, A.E., Nadelhffer, K.J. & Laundre, J.A. (1995) Responses of
558 arctic tundra to experimental and observed changes in climate. *Ecology*, **76**, 694-711.

559

560 Clausen, J., Keck D.D. & Hiesey, W.M. (1940) Experimental studies on the nature of species.

561 I. The effect of varied environments on western American plants. Washington, DC,

562 Carnegie Institute of Washington.

563

564 Clausen, J., Keck, D.D. & Hiesey, W.M. (1948) Experimental studies on the nature of species.

565 III. Environmental responses of climatic races of *Achillea*. Washington, DC, Carnegie

566 Institute of Washington.

567

568 Crispo, E. (2007) The Baldwin effect and genetic assimilation: Revisiting two mechanisms

569 of evolutionary change mediated by phenotypic plasticity. *Evolution*, 61, 2469-2479.

570

571 Crispo, E., DiBattista, J.D., Correa, C., Thibert-Plant, X., McKellar, A.E., Schwartz, A.K., Berner,

572 D. De Leon, L.F. & Hendry, A.P. (2010) The evolution of phenotypic plasticity in

573 response to anthropogenic disturbance. *Evolutionary Ecology Research*, **12**, 47-66.

574

575 Davis, M.B. & Shaw, R.G. (2001) Range shifts and adaptive responses to Quaternary climate

576 change. *Science*, **292**, 673-679.

577

578 De Witt, T.J., Sih, A. & Wilson, D.S. (1998) Costs and limits of phenotypic plasticity. *Trends in*

579 *Ecology and Evolution*, **13**, 77-81.

580

581 Fetcher, N. & Shaver, G.R. (1982) Growth and tillering patterns within tussocks of

582 *Eriophorum vaginatum*. *Holarctic Ecology*, **5**, 180-186.

583

584 Fetcher, N. & Shaver, G.R. (1983) Life histories of tillers of *Eriophorum vaginatum* in

585 relation to tundra disturbance. *Journal of Ecology*, **71**, 131-147.

586

587 Fetcher, N. & Shaver, G.R. (1990) Environmental sensitivity of ecotypes as a potential
588 influence on primary productivity. *The American Naturalist*, **136**, 126-131.

589

590 Finlay, K.W. & Wilkinson, G.N. (1963) The analysis of adaptation in a plant-breeding
591 programme. *Australian Journal of Agricultural Research*, **14**, 742-754.

592

593 Galen, C., Shore, J.S. & Deyoe, H. (1991) Ecotypic divergence in alpine *Polemonium*
594 *viscosum*: Genetic structure, quantitative variation, and local adaptation. *Evolution*, **45**,
595 1218-1228.

596

597 Ghalambor, C.K., McKay, J.K., Carroll, S.P. & Reznick, D.N. (2007) Adaptive versus non-
598 adaptive phenotypic plasticity and the potential for contemporary adaptation in new
599 environments. *Functional Ecology*, **21**, 394-407.

600

601 Gienapp, P., Teplitsky, C., Alho, J.S., Mills, J.A. & Merilä, J. (2008) Climate change and
602 evolution: disentangling environmental and genetic responses. *Molecular Ecology*, **17**,
603 167-178.

604

605 Gonzalo-Turpin, H. & Hazard, L. (2009) Local adaptation occurs along altitudinal gradient
606 despite the existence of gene flow in the alpine plant species *Festuca eskia*. *Journal of*
607 *Ecology*, **97**, 742-751.

608

- 609 Grime J.P. (1977) Evidence for the existence of three primary strategies in plants and its
610 relevance to ecological and evolutionary theory. *American Naturalist*, **111**, 169–1194.
611
- 612 Grime, J.P., Crick, J.C. & Rincon, J.E. (1986) The ecological significance of plasticity. In D.H.
613 Jennings and A.J. Trewavas (eds) *Plasticity in Plants*. Company of Biologists, Cambridge
614 University Press, Cambridge.
615
- 616 Haloin, J.R. & Strauss, S.Y. (2008) Interplay between ecological communities and evolution.
617 *Annals of the New York Academy of Sciences*, **1133**, 87-125.
618
- 619 Hendry, A.P., Kinnison, M.T., Heino, M., Day, T., Smith, T.B., Fitt, G., Bergstrom, C.T.,
620 Oakeshott, J., Jorgensen, P.S., Zalucki, M.P., Gilchrist, G., Southeron, S., Sih, A., Strauss, S.,
621 Denison, R.F. & Carroll, S.P. (2011) Evolutionary principles and their practical
622 application. *Evolutionary Applications*, **4**,159-183.
623
- 624 Hereford, J. (2009) A quantitative survey of local adaptation and fitness trade-offs. *The*
625 *American Naturalist*, **173**, 579-588.
626
- 627 Hinzman, L.D., Bettez, N.D., Bolton, W.R., Chapin, F.S., Dyurgerov, M.B. Fastie, C.L., Griffith,
628 B., Hollister, R.D., Hope, A., Huntington, H.P., Jensen, A.M., Jia, G.J., Jorgenson, T., Kane, D.
629 L., Klein, D. R., Kofinas, G., Lynch, A.H., Lloyd, A.H., McGuire, A.D., Nelson, F.E., Oechel,
630 W.C., Osterkamp, T.E., Racine, C.H., Romanovsky, V.E., Stone, R.S., Stow, D.A., Sturm, M.,
631 Tweedie, C.E., Vourlitis, G.L., Walker, M.D., Walker, D.A., Webber, P. J., Welker, J.M.,

- 632 Winker, K.S. & Yoshikawa, K. (2005) Evidence and implications of recent climate change
633 in Northern Alaska and other arctic regions. *Climatic Change*, **72**, 251-298.
634
- 635 Holt, R.D. (1990) The microevolutionary consequences of climate change. Trends in
636 *Ecology and Evolution*, **5**, 311-315.
637
- 638 Hu, F.S., Higuera, P.E., Walsk, J.E., Chapman, W.L. Duffy, P.A., Brubaker, L.B. & Chipman, M.L.
639 (2010) Tundra burning in Alaska: Linkages to climatic change and sea ice retreat.
640 *Journal of Geophysical Research – Biogeosciences*, **115**, G04002.
641
- 642 Hudson, J.M.G. & Henry, G.H.R. (2009) Increased plant biomass in a High Arctic heath
643 community from 1981 to 2008. *Ecology*, **90**, 2657-2663.
644
- 645 Hufford, K.M., Mazer, S.J. & Camara, M.D. (2008) Local adaptation and effects of grazing
646 among seedlings of two native California bunchgrass species: Implications for
647 restoration. *Restoration Ecology*, **16**, 59-69.
648
- 649 Hultén, E. (1959) Studies in the genus *Dryas*. *Svensk Botanisk Tidskrift*, **53**, 507-542.
650
- 651 Intergovernmental Panel on Climate Change. 2007. Climate Change 2007: The Physical
652 Science Basis. Summary for Policy Makers – A Report of Working Group II of the
653 Intergovernmental Panel on Climate Change. Fourth Assessment Report. IPCC, Paris,
654 France.

655

656 Joshi, J., Schmid, B., Caldeira, M.C., Dimitrakopoulos, P.G., Good, J., Harris, R., Hector, A.,
657 Huss-Danell, K., Jumpponen, A., Minns, A., Mulder, C.P.H., Pereira, J.S., Prinz, A., Scherer-
658 Lorenzen, M., Siamantziouras, A-S.D., Terry, A.C., Troumbis, A.Y. & Lawton, J.H. (2001)
659 Local adaptation enhances performance of common plant species. *Ecology Letters*, **4**,
660 536-544.

661

662 Jump, A.S. & Penuelas, J. (2005) Running to stand still: adaptation and the response of
663 plants to rapid climate change. *Ecology Letters*, **8**, 1010-1020.

664

665 van Kleunen, M. & Fischer, M. (2005) Constraints on the evolution of adaptive phenotypic
666 plasticity in plants. *New Phytologist*, **166**, 49-60.

667

668 Knight, C.A., Vogel, H., Kroymann, J., Shumate, A., Witsenboer, H., & Mitchell-Olds, T. (2006)
669 Expression profiling and local adaptation of *Boechera holboellii* populations for water
670 use efficiency across a naturally occurring water stress gradient. *Molecular Ecology*, **15**,
671 1229-1237.

672

673 Lacaze, X., Hayes, P.M. & Korol, A. (2009) Genetics of phenotypic plasticity: QTL analysis in
674 barley, *Hordeum vulgare*. *Heredity*, **102**, 163-173.

675

- 676 Levin, D.A. (1988) Plasticity, canalization and evolutionary stasis in plants. Pages 35–45 in
677 A. J. Davy, M. J. Hutchings, and A. R. Watkinson, eds. *Plant population ecology*. Blackwell
678 Scientific, Oxford.
- 679
- 680 Liancourt, P. & Tielborger, K. (2009) Competition and a short growing season lead to
681 ecotypic differentiation at the two extremes of the ecological range. *Functional Ecology*,
682 **23**, 397-404.
- 683
- 684 Li, B., Suzuki, J-I. & Hara, T. (1998) Latitudinal variation in plant size and relative growth
685 rate in *Arabidopsis thaliana*. *Oecologia*, **115**, 293-301.
- 686
- 687 Linhart, Y.C. & Grant, M.C. (1996) Evolutionary significance of local differentiation in plants.
688 *Annual Review of Ecology and Systematics*, **27**, 237-277.
- 689
- 690 Mark, A.F., Fetcher, N., Shaver, G.R. & Chapin, F.S. III (1985) Estimated ages of mature
691 tussocks of *Eriophorum vaginatum* along a latitudinal gradient in Central Alaska, U.S.A.
692 *Arctic and Alpine Research*, **17**, 1-5.
- 693
- 694 McGraw, J.B. & Antonovics, J. (1983a) Experimental ecology of *Dryas octopetala* ecotypes.
695 I. Ecotypic differentiation and life cycle stages of selection. *Journal of Ecology*, **71**, 879-
696 897.
- 697

- 698 McGraw, J.B. & Antonovics, J. (1983b) Experimental ecology of *Dryas octopetala* ecotypes.
699 II. A demographic model of growth, branching and fecundity. *Journal of Ecology*, **71**,
700 899-912.
- 701
- 702 McGraw, J.B. & Shaver, G.R. (1982) Seedling density and seedling survival in Alaskan cotton
703 grass tussock tundra. *Holarctic Ecology* **5**, 212-217.
- 704
- 705 McGraw, J.B., Chester, A.L. & Stuart, L. (1983) A note on July senescence in tundra plants at
706 Eagle Creek, Alaska, U.S.A. *Arctic and Alpine Research*, **15**, 267-269.
- 707
- 708 McGraw, J.B. (1987) Experimental ecology of *Dryas octopetala* ecotypes. IV. Fitness
709 response to reciprocal transplanting in ecotypes with differing plasticity. *Oecologia*, **73**,
710 465-468.
- 711
- 712 McGraw, J.B. & Fetcher, N. (1992) Response of tundra plant populations to climatic change.
713 In, Arctic ecosystems in a changing climate: An ecophysiological perspective (F.S.
714 Chapin *et al.*, eds) Academic Press, pp. 359-376.
- 715
- 716 Miglia, K.J., McArthur, E.D., Moore, W.S., Wang, H., Graham, J.H. & Freeman, D.C. (2005)
717 Nine-year reciprocal transplant experiment in the gardens of the basin and mountain
718 big sagebrush (*Artemisia tridentate*: Asteraceae) hybrid zone of Salt Creek Canyon: the
719 importance of multiple-year tracking of fitness. *Biological Journal of the Linnean*
720 *Society*, **86**, 213-225.

- 721
- 722 Miller, P.C. (1982) Environmental and vegetational variation across a snow accumulation
723 area in montane tundra in central Alaska. *Holarctic Ecology*, **5**, 85-98.
- 724
- 725 Mooney, E.H. & Billings, W.D. (1961) Comparative physiological ecology of arctic and alpien
726 populations of *Oxyria digyna*. *Ecological Monographs*, **31**, 1-29.
- 727
- 728 Nicotra, A.B., Atkin, O.K., Bonser, S.P., Davidson, A.M., Finnegan, E.J., Mathesius, U., Poot, P.,
729 Purugganan, M.D., Richards, C.L., Valladares, F. & van Kleunen, M. (2010) Plant
730 phenotypic plasticity in a changing climate. *Trends in Plant Science*, **15**, 684-692.
- 731
- 732 Parmesan, C. (2006) Ecological and evolutionary responses to recent climate change.
733 *Annual Review of Ecology, Evolution and Systematics*, **37**, 637-669.
- 734
- 735 Pfenning, D.W., Wund, M.A., Snell-Rood, E.C., Cruickshank, T., Schlichting, C.D. & Moczek,
736 A.P. (2010) Phenotypic plasticity's impacts on diversification and speciation. *Trends in*
737 *Ecology and Evolution*, **25**, 459-467.
- 738
- 739 Pigliucci, M. (2007) Do we need an extended evolutionary synthesis? *Evolution*, **61**, 2743-
740 2749.
- 741
- 742 Primack, R.B. & Kang, H. (1989) Measuring fitness and natural selection in wild plant
743 populations. *Annual Review of Ecology and Systematics*, **20**, 367-396.

- 744
- 745 Richards, C.L., Bossdorf, O., Muth, N.Z., Gurevitch, J., and Pigliucci, M. (2006) Jack of all
746 trades, master of some? On the role of phenotypic plasticity in plant invasions. *Ecology*
747 *Letters* **9**, 981-993.
- 748
- 749 Rutter, M.T. & Fenster, C.B (2007) Testing for adaptation to climate in *Arabidopsis thaliana*:
750 a calibrated common garden approach. *Annals of Botany*. **99**, 529-536.
- 751
- 752 Sambatti, J.B.M. & Rice, K.J. (2006) Local adaptation, patterns of selection, and gene flow in
753 the Californian serpentine sunflower (*Helianthus exilis*). *Evolution*, **60**, 696-710.
- 754
- 755 Santamaria, L., Figuerola, J., Pilon, J.J., Mjelde, M., Green, A.J., de Boer, T., King, R.A. & Gornall,
756 R.J. (2003) Plant performance across latitude: The role of plasticity and local
757 adaptation in an aquatic plant. *Ecology*, **84**, 2454-2461.
- 758
- 759 Schlichting, C.D. (1986) The evolution of phenotypic plasticity in plants. *Annual Review of*
760 *Ecology and Systematics*. **17**, 667-693.
- 761
- 762 Schlichting, C.D. (2004) The role of phenotypic plasticity in diversification. In Phenotypic
763 Plasticity: Functional and Conceptual Approaches (DeWitt, T.J. and Scheiner, S.M., eds),
764 pp. 191–200, Oxford University Press.
- 765
- 766 Schwaegerle, K.E., McIntyre, H. & Swingley, C. (2000) Quantitative genetics and the

- 767 persistence of environmental effects in clonally propagated organisms. *Evolution*, **54**:
768 452-461.
- 769
- 770 Shaver, G.R., Chapin, F.S. III & Billings, W.D. (1979) Ecotypic differentiation in *Carex*
771 *aquatilis* as related to icewedge polygonization in the Alaskan coastal tundra. *Journal of*
772 *Ecology*, **67**, 1025-1046.
- 773
- 774 Shaver, G.R., Fetcher, N. & Chapin, F.S. III (1986) Growth and flowering in *Eriophorum*
775 *vaginatum*: annual and latitudinal variation. *Ecology*, **67**, 1524-1535.
- 776
- 777 Shaver, G.R. & Laundre, J. (1997) Exsertion, elongation, and senescence of leaves of
778 *Eriophorum vaginatum* and *Carex bigelowii* in northern Alaska. *Global Change Biology*, **2**
779 (Suppl. 1), 146-157.
- 780
- 781 Shimono, Y., Watanabe, M., Hirao, A.S., Wada, N. & Kudo, G. (2009) Morphological and
782 genetic variations of *Potentilla matsumarae* (Rosaceae) between fellfield and snowbed
783 populations. *American Journal of Botany*, **96**, 728-737.
- 784
- 785 Sokal, R.R. & Rohlf, F.J. (1981) Biometry: The Principles and Practice of Statistics in
786 Biological Research (2nd ed.) W.H. Freeman and Company, NY.
- 787
- 788 Sonesson, M., Sveinbjörnsson, B., Tehler, A. & Carlsson, B.Å. (2007) A comparison of the
789 physiology, anatomy and ribosomal DNA in alpine and subalpine populations of the

- 790 lichen *Nephroma arcticum*—the effects of an eight-year transplant experiment. *The*
791 *Bryologist*, **110**,244-253.
- 792
- 793 Souther, S. & McGraw, J.B. (2011) Evidence of local adaptation in the demographic response
794 of American ginseng to interannual temperature variation. *Conservation Biology*, **25**,
795 922-931.
- 796
- 797 Sturm, M., Racine, C. & Tape, K. (2001) Increasing shrub abundance in the arctic. *Nature*,
798 **411**, 546-547.
- 799
- 800 Sultan, S.E. & Spencer, H.G. (2002) Metapopulation structure favors plasticity over local
801 adaptation. *The American Naturalist*, **160**, 271-283.
- 802
- 803 Tape, K., Sturm, M. & Racine, C. (2006) The evidence for shrub expansion in Northern
804 Alaska and the Pan-Arctic. *Global Change Biology*, **12**, 686-702.
- 805
- 806 Thuiller, W., Albert, C., Araújo, M.B., Berry, P.M., Cabeza, M., Guisan, A., Hickler, T., Midgley,
807 G.F., Paterson, J., Schurr, F.M., Sykes, M.T. & Zimmermann, N.E. (2008) Predicting global
808 change impacts on plant species' distributions: Future challenges. *Perspectives in Plant*
809 *Ecology, Evolution and Systematics*, **9**, 137-152.
- 810
- 811 Van Valen, L. (1965) Morphological variation and width of ecological niche. *American*
812 *Naturalist*, **99**, 377-390.

813

814 Visser, M.E. (2008) Keeping up with a warming world; assessing the rate of adaptation to
815 climate change. *Proceedings of the Royal Society Biological Sciences*, **275**, 649-659.

816

817 Walker, M.D., Wahren, C.H., Hollister, R.D., Henry, G.H.R., Ahlquist, L.E., Alatalo, J.M., Bret-
818 Harte, M.S., Calef, M.P., Callaghan, T.V., Carroll, A.B., Epstein, H.E., Jonsdottir, I.S., Klein,
819 J.A., Magnusson, B., Molau, U., Oberbauer, S.F., Rewa, S.P., Robinson, C.H., Shaver, G.R.,
820 Suding, K.N., Thompson, C.C., Tolvanen, A., Totland, O., Turner, P.L., Tweedie, C.E.,
821 Webber, P.J. & Wookey, P.A. (2006) Plant community responses to experimental
822 warming across the tundra biome. *Proceedings of the National Academy of Sciences*,
823 **103**, 1342-1346.

824

825 West-Eberhard, M.J. (2005) Developmental plasticity and the origin of species differences.
826 *Proceedings of the National Academy of Sciences*, **102**(Suppl. 1), 6543-6549.

827

828 Wright, J.W. (2007) Local adaptation to serpentine soils in *Pinus ponderosa*. *Plant and Soil*,
829 **293**, 209-217.

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

833

Effect	d.f.	Level	Survival			Number of Flowers (per shoot)			Number of Shoots		
			%	χ^2	<i>P</i>	Mean	F	<i>P</i>	Mean	F	<i>P</i>
		Fellfield	63	14.85	<0.001	0.015	1.67	0.20	110.58	4.36	0.02
Garden	2	Intermediate	70			0.016			84.65		
		Snowbed	27			0.045			8.47		
Origin	1	Home	77	12.68	<0.001	0.031	0.65	0.43	71.57	0.08	0.78
		Away	42			0.020			64.23		

834

835

Table 2. Results of analyses comparing survival and flower number

836

of *E. vaginatum* genotypes in each of six gardens created along a

837

latitudinal gradient in interior Alaska

Effect	d.f.	Survival		Number of Flowers	
		χ^2	<i>P</i>	F	<i>P</i>
Garden	5	3.33	0.65	8.04	<0.0001
Origin	1	8.28	0.004	34.70	<0.0001
Garden x Origin	5	11.25	0.047	6.41	<0.0001

838

839

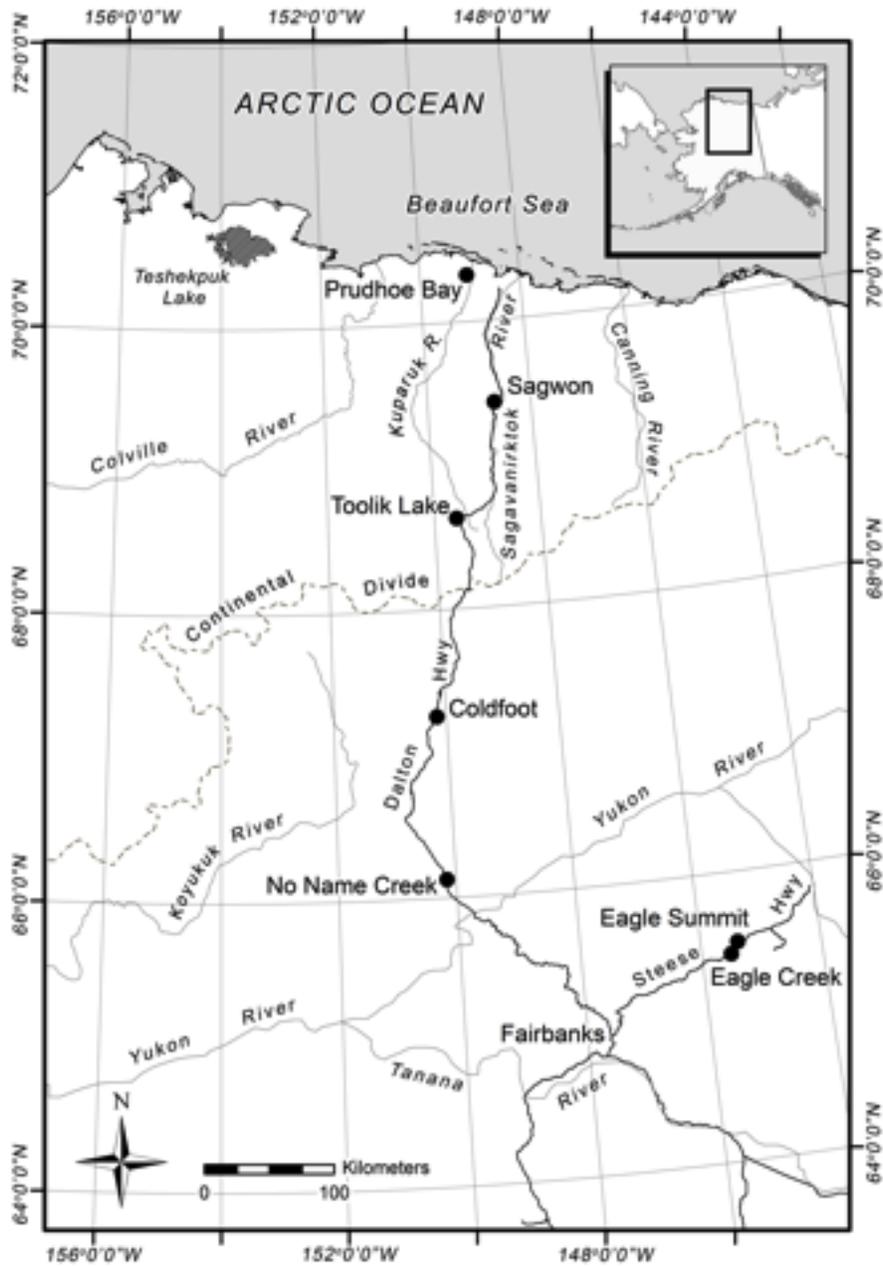
840
841

842 Table 3 Slopes of regressions of Population mean tiller index value on Garden mean tiller
843 index value for *E. vaginatum* tiller index from six reciprocal transplant gardens in interior
844 Alaska. Values of the t statistic, and associated *P* values, test the null hypothesis that $\beta = 1$,
845 or the mean slope.

		Eagle Creek	No Name Creek	Coldfoot	Toolik Lake	Sagwon	Prudhoe Bay
1993	Slope, β	1.91	1.52	1.19	0.60	0.22	0.30
	t	5.69	2.73	0.78	-2.54	-4.85	-4.96
	<i>P</i>	0.002	0.041	0.471	0.052	0.005	0.004
2010	Slope, β	1.34	1.16	1.23*	0.68	0.51	0.50
	t	3.06	1.29	1.59	-3.44	-4.95	-5.82
	<i>P</i>	0.028	0.254	0.273	0.018	0.004	0.002

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

848

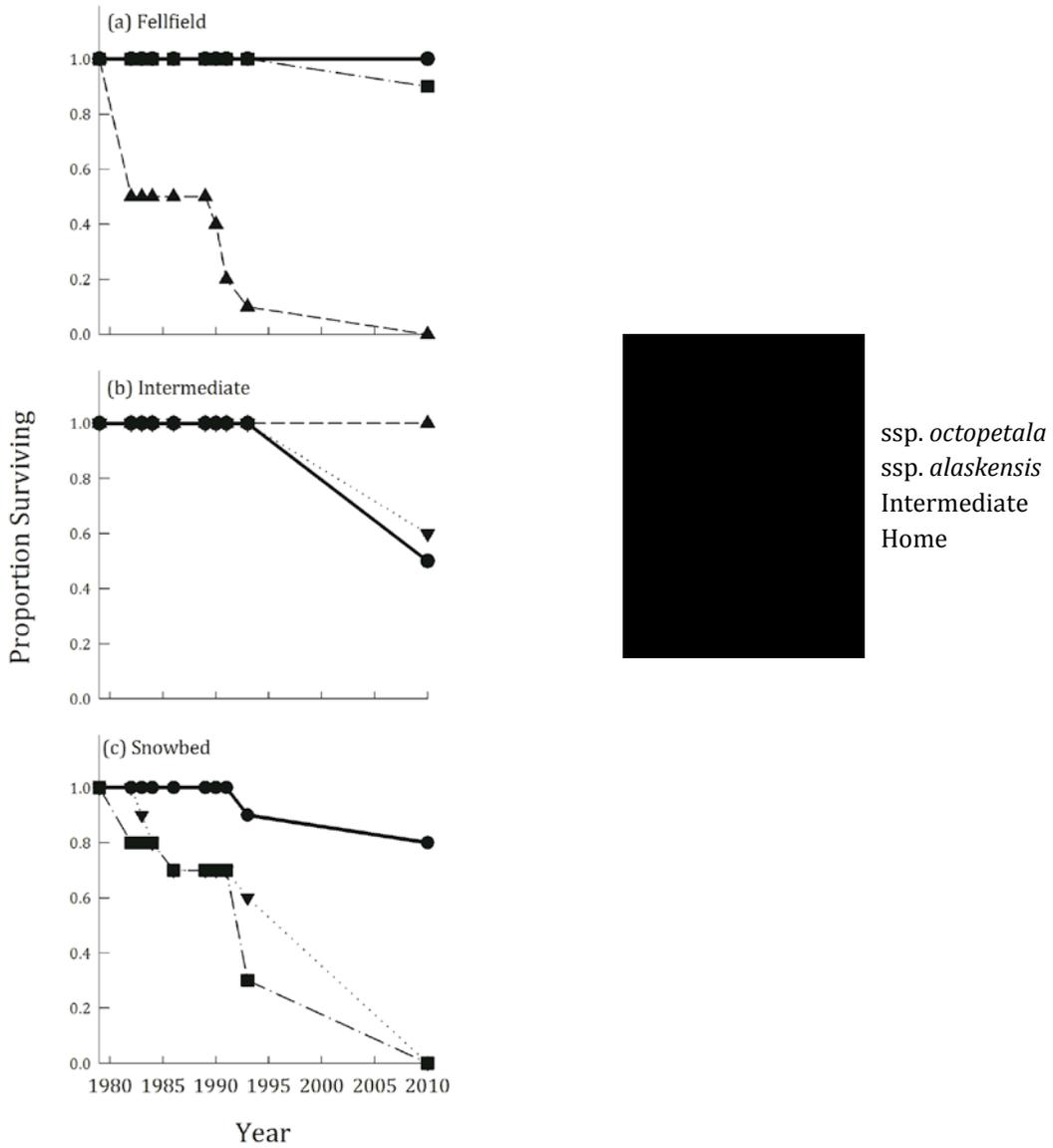


849

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

853

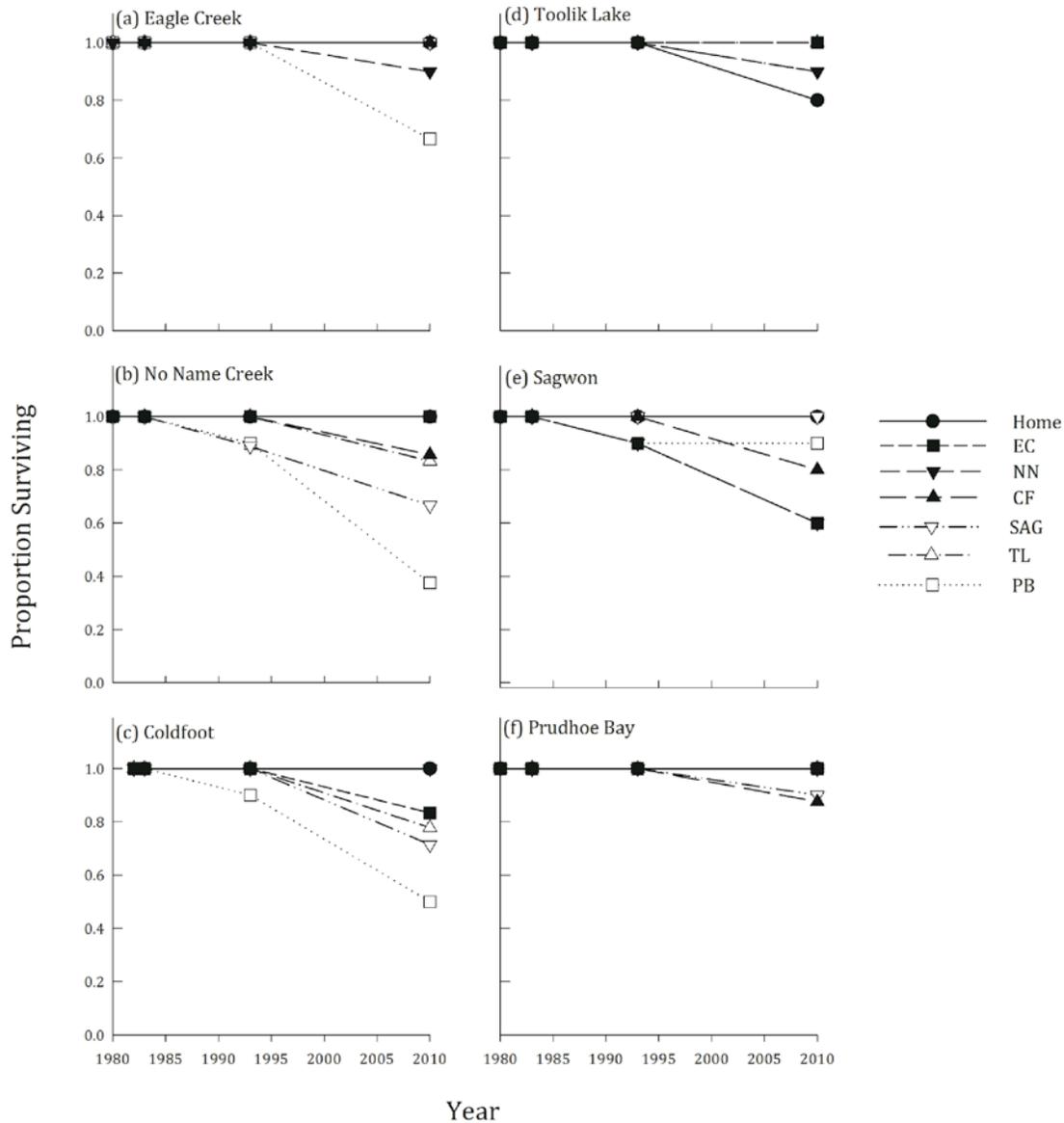
854



855

856 Fig. 2. Survival (%) of three forms of *Dryas octopetala* (*ssp. octopetala*, *ssp. alaskensis*, and
 857 their intermediate) over 31 years when planted in a reciprocal transplant experiment in a)
 858 fellfield, b) intermediate, and c) snowbed sites. In each graph, survival of the home ecotype
 859 is illustrated as the solid black line with filled circles.

860



861

862

Fig. 3. Survival of reciprocally transplanted *Eriophorum vaginatum* tussocks from six

863

populations (Coldfoot, CF; No Name Creek, NN; Eagle Creek, EC; Toolik Lake, TL; Sagwon,

864

SAG; and Prudhoe Bay, PB) over 30 years in gardens created at a) CF, b) NN, c) EC, d) TL, e)

865

SAG, and f) PB sites. In each graph, survival of the home ecotype is illustrated as the solid

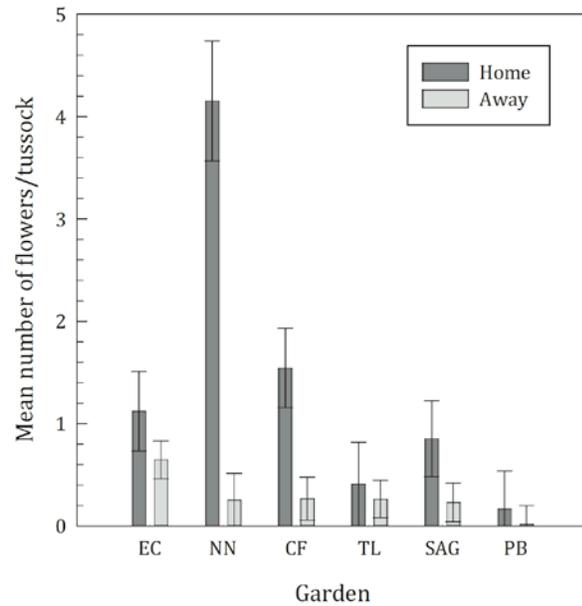
866

black line with filled circles. In many cases, overlapping lines prevent all lines from being

867

observable on graphs.

868



869

870 Fig. 4. Mean number of flowers (± 1 SE) produced in 2010 by *Eriophorum vaginatum*

871 tussocks that were reciprocally transplanted into six garden sites (Coldfoot, CF; No Name

872 Creek, NN; Eagle Creek, EC; Toolik Lake, TL; Sagwon, SAG; and Prudhoe Bay, PB) in 1980–

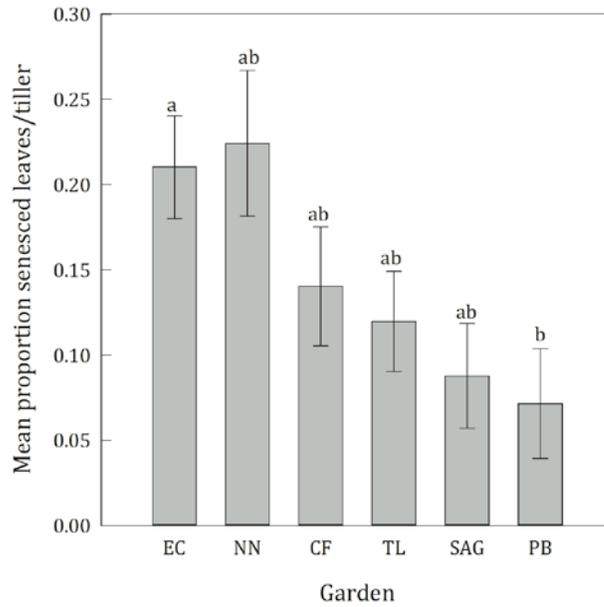
873 1982. Home tussock means were calculated for tussocks that originated from a particular

874 Garden site while Away tussock means were calculated from all tussocks that originated in

875 sites other than the indicated Garden.

876

877



878

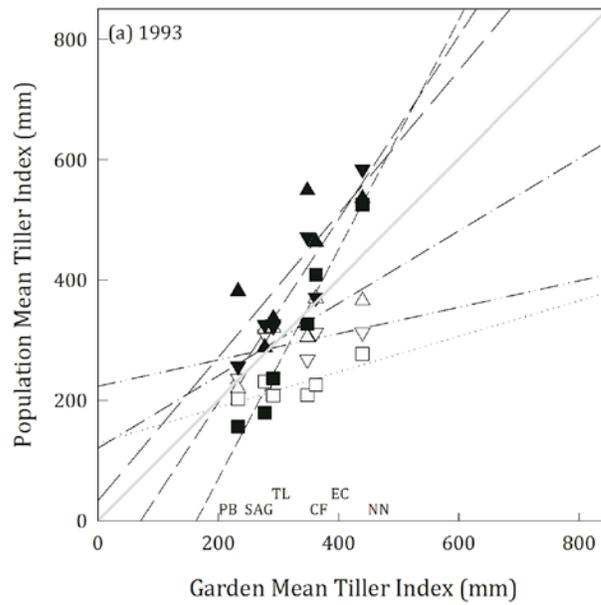
879 Fig. 5. Mean proportion of *Eriophorum vaginatum* leaves per tiller that were 25% or 50%

880 senesced when reciprocally transplanted tussocks were censused in July 2010. Means

881 were calculated across tussocks that were originally from all six sites in each garden.

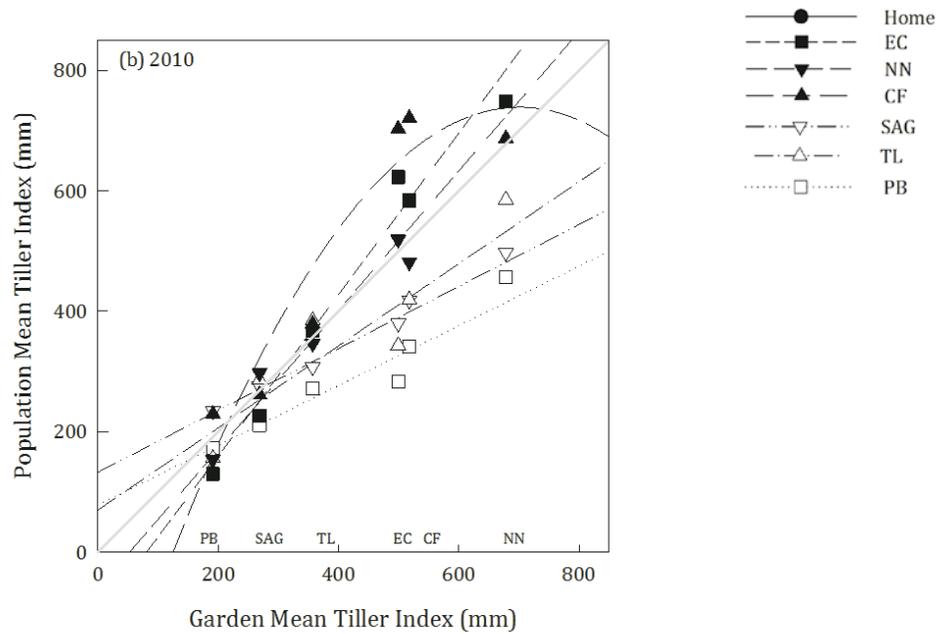
882

883



884

885



886

887 Fig. 6. Tiller-size index (length of the longest leaf (mm) multiplied by the number of green

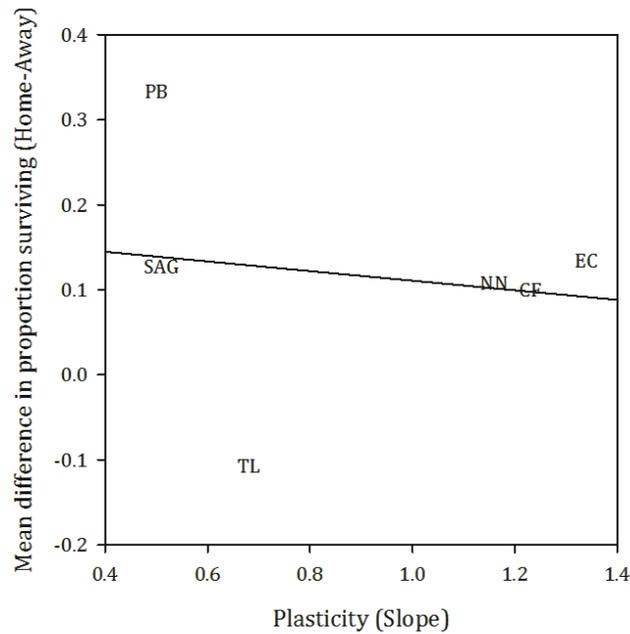
888 leaves) for each of six populations (Coldfoot, CF; No Name Creek, NN; Eagle Creek, EC;

889 Toolik Lake, TL; Sagwon, SAG; and Prudhoe Bay, PB) of *Eriophorum vaginatum* grown in

890 each of the six sites regressed on the mean tiller index of tussocks from all populations at

891 each site. Lines were fitted by least-squares regression. The solid gray line illustrates the
892 mean slope of one. The slope of the line for each population is a measure of its plasticity.
893

894



895
 896 Fig. 7. Difference in the proportional survival between tussocks of *Eriophorum vaginatum*
 897 planted in Home and Away gardens regressed against the mean plasticity of tussocks from
 898 each population (Coldfoot, CF; No Name Creek, NN; Eagle Creek, EC; Toolik Lake, TL;
 899 Sagwon, SAG; and Prudhoe Bay, PB) where plasticity was measured as the slope of the line
 900 relating genotypic and environmental values for tiller index.

901

902

903