Experimental ecology of *Dryas octopetala* ecotypes

IV. Fitness response to reciprocal transplanting in ecotypes with differing plasticity

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Summary. Growth, survival and reproduction of adult plants from three reciprocally-transplanted populations of *Dryas octopetala* were followed over a seven year period, from 1979 to 1986. The two most different ecotypes, from snowbed and fellfield environments, were strongly selected against in extreme foreign environments *via* differential growth, survival, and reproduction. The more phenotypically-plastic ecotype from the snowbed experienced rapid, early mortality on the fellfield, prior to morphological adjustment, but no mortality in the last five years of the experiment. The less plastic fellfield ecotype showed no mortality for the first three years followed by a steady decline in numbers for the next four years. The ecotypic difference in plasticity may account for the contrasting mortality patterns. A population of plants with intermediate morphology was intermediate in fitness in extreme environments, but showed no superiority in its home site, suggesting that it is not a locally-adapted population. Natural selection maintains genetic differences between snowbed and fellfield populations in the face of gene flow. However, based on the response of intermediates, there appear to be limits to the degree to which selection can fine-tune adaptation along environmental gradients.

Key words: *Dryas octopetala* – Ecotypes – Selection – Plasticity

Plant species are frequently comprised of genetically-differentiated populations (ecotypes), each of which is adapted to a different set of environmental conditions. Such genetic differentiation has been documented extensively and appears to be the rule rather than the exception in plants (see Heslop-Harrison 1964 and Langlet 1971 for reviews). Where genetically-distinct populations are found in adjacent habitats, theoretical studies show that gene flow will tend to obliterate genetic differences unless counteracted by strong selection (Jain and Bradshaw 1966). *Dryas octopetala* is a widespread dwarf shrub species that contains such adjacent, genetically-distinct populations (McGraw and Antonovics 1983a). Although *D. octopetala* typically occurs on rocky fellfields, within mountains in Alaska its range includes snowbeds (McGraw and Antonovics 1983a). Field and growth chamber studies have shown that snowbed plants differ from fellfield plants in quantitative traits and that snowbed plants have a competitive advan-

tage over fellfield plants in the relatively resource-rich snowbed environment (McGraw 1985a, 1985b). One purpose of the present study was to determine experimentally whether, and how strongly, natural selection acts to maintain genetic differences among adjacent populations of *D. octopetala*. This was done in the context of a classical reciprocal transplant study in which growth, survival, and reproduction were followed during a seven-year period.

One of the important differences between snowbed and fellfield plants is their degree of morphological plasticity in response to the gradient from snowbed to fellfield (McGraw and Antonovics 1983a). Snowbed plants are phenotypically plastic, especially in size-related traits such as leaf dimensions, while fellfield plants are morphologically stable across the same environmental gradient. Although the evolution of such plasticity differences has been demonstrated repeatedly (see Bradshaw 1965; Schlichting 1986, for reviews), few studies have examined the consequences of differing amounts of plasticity. In this study, I hypothesized that the more plastic snowbed plants should experience a reduced rate of selection in the fellfield environment as morphological adjustment to the environment proceeds. Fellfield plants, in contrast, were expected to have a relatively constant pattern of selection over time, consistent with their unchanging morphology.

A third issue of interest in this study was the degree to which selection "fine tunes" the distribution of contrasting genotypes along the gradient from fellfield to snowbed. In particular, I asked whether plants that were morphologically intermediate between snowbed and fellfield plants represented a third locally-adapted ecotype, or whether they were hybrids that occasionally survived in intermediate sites where selection was weak. A lack of local adaptation may indicate that there are limits to the ability of natural selection to fine-tune the distribution of genotypes among environments (Schwagerle and Bazzaz 1987).

Materials and methods

Study site and species

The field site was located near Mile 106 on the Steese Highway northeast of Fairbanks, Alaska, USA. (65°26′N, 145°30′W). The site consists of a snow-free ridgetop (fellfield) and a snowbank in a concave slope below the ridge (McGraw and Antonovics 1983a). The fellfield has mineral soils low in nutrient availability, is exposed to high winds

and snowblast in winter, and has sparse vegetative cover. In contrast, the snowbed has well-drained organic soils with relatively high nutrient availability, more dense vegetation, an abbreviated growing season, and is protected by snow-cover in winter. Detailed environmental measurements and vegetation descriptions are reported elsewhere (Miller 1982; Alpert and Oechel 1982; Miller et al. 1982; Murray and Miller 1982; McGraw and Antonovics 1983a; McGraw 1985a).

On the fellfield, *Dryas octopetala* ssp. *octopetala* is the dominant form, while in the snowbed, less than 100 m away, ssp. *alaskensis* predominates (nomenclature follows Hulten 1968). Between the fellfield and snowbed, plants with intermediate morphology occur next to individuals of either subspecies. The two extreme forms have been termed ecotypes (*sensu* Turesson 1922; McGraw and Antonovics 1983a). They are cross-compatible, yet morphological differences between them are pronounced: The fellfield ecotype has small (5–15 mm), deciduous, variously-pubescent leaves and a compact, mat-like shrub growth form. The snowbed ecotype has larger (15–50 mm) evergreen, glabrous leaves and a more extensive, clonal shrub growth form.

Reciprocal transplant study

In late July, 1979, adult plants of the fellfield, intermediate, and snowbed populations were transplanted in all possible combinations to fellfield, forb-grass (henceforth called "intermediate") and Lower Dryas (henceforth called "snowbed") sites in a classical reciprocal transplant experimental design. In each site, ten replicates from each population were transplanted for a total of 90 transplants. Some soil was transferred with the plants to minimize root damage, and a 2–4 cm wide zone was cleared of vegetation around each plant. Transplants were watered once and allowed to become established.

Survival of all plants in each garden was assessed with censuses in the summers of 1980, 1981, 1982, 1983, 1984, and 1986. A plant was considered dead when it no longer had living leaves.

Individual plant size was measured at the level of the shoot module (defined here as the apical meristem and all live leaves produced by that meristem; McGraw and Antonovics 1983b). Plant growth (change in plant size) was determined by the change in the number of shoots comprising the individual plant. This measure is particularly useful because in *D. octopetala* shoot population size is highly correlated with potential fecundity (McGraw and Antonovics 1983b). Therefore, if a plant is found to be increasing in shoot population number, it is also increasing its potential reproductive output, and vice-versa.

Ten randomly-chosen shoots on each plant were marked in August, 1979 with numbered jewelry tags for a total of 900 shoots. Shoots were censused again in 1980 and 1981 with notations of survival and branching. By 1982, many tags were either unreadable or had disintegrated. Therefore in recensusing in 1984 and 1986, total shoot numbers on each plant were counted. Growth from 1979–1981 and from 1984–1986 was expressed in terms of relative change in shoot numbers for each plant. Two-way analyses of variance were performed to determine the main effects of site and ecotype on growth, and to determine

whether there was an ecotypic difference in response to site (an ecotype × site interaction).

Total flower number was counted in 1984 and 1986 on each plant. Because few plants flowered, a formal analysis of variance could not be done, however a two-way contingency analysis (with a G-test, Sokal and Rohlf 1981) was performed to determine whether there was an interaction between ecotype and site in the fraction of plants that flowered. Because there was no flowering in some site-population combinations, the actual analysis was carried out on the proportion of plants that did not flower.

Results

Survival rates of reciprocally-transplanted adults of *D. octopetala* were strikingly different over the long-term than those reported previously for the first two years of the experiment (McGraw and Antonovics 1983a). In particular, the snowbed ecotype, which showed high mortality at the fellfield site early on (1979–1981), showed no mortality over the ensuing five years (Fig. 1). In addition, although no mortality of fellfield plants was observed in the snowbed in the first three years, a steady decline in numbers occurred in the fourth through seventh years. Mortality of intermedi-
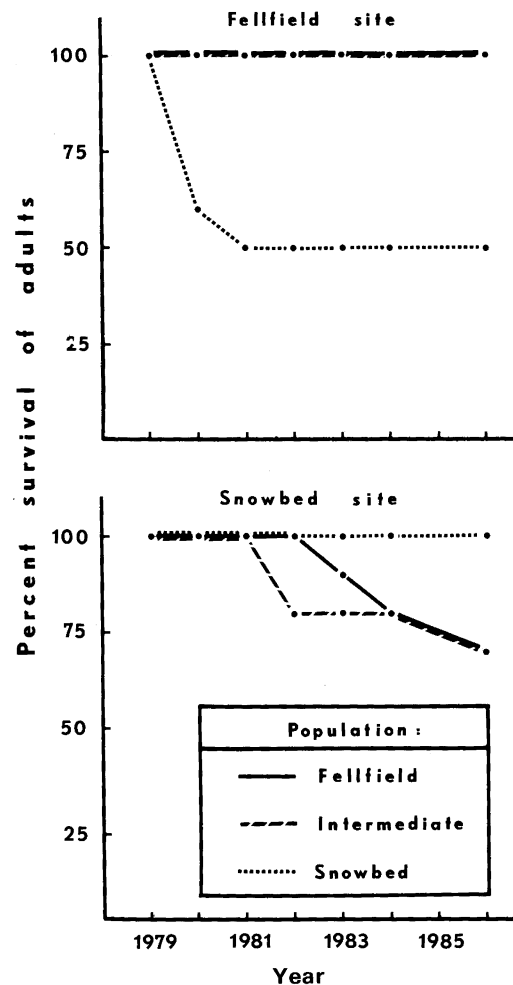

Fig. 1. Survival of *D. octopetala* populations over 7 years in snowbed and fellfield sites. Survival was 100% for all populations at the intermediate site; these data are not shown
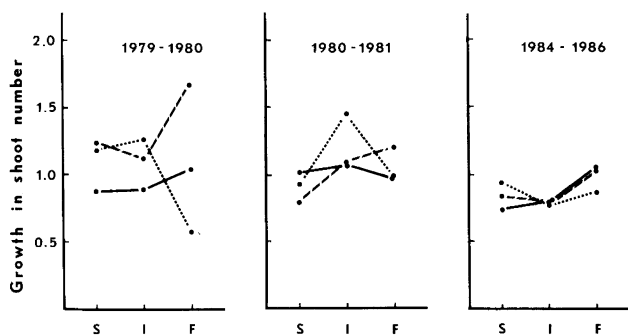
Fig. 2. Changes in the number of shoots in the reciprocal transplant experiment expressed as (number of shoots at end of interval)/ (number of shoots at beginning of interval)

Table 1. Number of flowering individuals in 1986 in the reciprocal transplant experiment

Year	Population	Site		
		Fellfied	Intermediate	Snowbed
1984	Fellfield	0	2	0
	Intermediate	3	4	3
	Snowbed	0	2	2
1986	Fellfield	1	2	0
	Intermediate	5	4	0
	Snowbed	0	2	2

ate plants (from the intermediate site) paralleled that of fellfield plants in the snowbed site, although it began one year earlier. No mortality occurred in the intermediate site in any year.

Shoot population growth rates varied significantly among ecotypes, sites, and years at various times (Fig. 2). In addition, there were significant differences in the response of ecotypes to the gradient of sites. In the first year following transplanting (1979–1980), ecotypes generally had high shoot population growth rates in *"home"* sites, although intermediate plants did not follow this pattern. For snowbed and intermediate plants, growth rates tended to increase with transplanting to the next higher zone on the snowbank gradient. The difference between ecotypes in response to site was revealed as a significant ecotype × site interaction ($P<0.01$, 2-way ANOVA).

In the second year (1980–1981) the ecotype-site interaction was not significant, although sites were different, with the greatest growth being found in the intermediate site for snowbed and fellfield populations ($P<0.01$, 2-way ANOVA). For the fellfield and snowbed sites and ecotypes, the pattern of variation across sites was the reverse of that expected based on their natural distributions: Although means were not significantly different, the fellfield plants tended to have a higher growth rate in the snowbed and the snowbed plants tended to have a higher population growth rate in the fellfield. Over the two-year period (1979–1981), the ecotype × site interaction remained significant ($P<0.01$, 2-way ANOVA) due to the over-riding effects of the first year.

By 1984–1986, shoot population growth rates were much less variable across sites and ecotypes. Shoot population growth rates were greatest for "home" ecotypes in fellfield and snowbed sites, Moreover, at fellfield and snowbed sites, growth of intermediate plants was between that of fellfield and snowbed plants. At the intermediate site, growth over two years was virtually identical for all ecotypes. Excluding the intermediate population from the analysis, there was a significant ecotype × site interaction in shoot population growth ($P<0.05$, 2-way ANOVA). In snowbed and fellfield sites, shoot population growth rates of alien plants were significantly less than one ($P<0.05$, t-test, both sites).

There was no significant interaction between site and ecotype in determining the fraction of individuals that flowered in 1984, however flowering of ecotypes did respond

differently to sites in 1986 (G-test, $P<0.01$). Specifically, flowering tended to be greatest for ecotypes in home sites or adjacent sites *vis-a-vis* ecotypes in distant alien sites (Table 1).

Discussion

After three growing seasons, differential survival of adult transplants had occurred only in the fellfield (McGraw and Antonovics 1983a), however after eight growing seasons mortality selection was evident at the snowbed site as well. The constant rate of mortality of fellfield and intermediate plants at the snowbed site over several years suggests this pattern may persist, eventually eliminating these plants from the site. In contrast, the high rate of mortality of snowbed plants at the fellfield site early on was followed by no further mortality in the last five years of the experiment.

The contrast between the timing of selection *via* differential mortality at fellfield and snowbed sites may be related to the difference in phenotypic plasticity between fellfield and snowbed plants (McGraw and Antonovics 1983a). In many respects (except leaf pubescence, gland characteristics, and degree of dissection), snowbed plants closely resembled fellfield plants in outward appearance after one year of acclimation to the fellfield site. The association between the change in mortality rate and change in phenotype suggests plasticity in itself may be an adaptive characteristic that prevents or delays further mortality of displaced snowbed plants. Fellfield plants were apparently not immediately stressed to the point of plant death at the snowbed site, but their lack of plasticity may account for the eventual steady rate of mortality at the snowbed site. Plasticity as observed in the snowbed population may have adaptive significance (see Bradshaw 1965 and Schlichting 1986, for reviews), but few examples are available where intra-specific variation in plasticity has been correlated with the temporal pattern of fitness response.

In the first two years in reciprocal transplant gardens, the patterns of selection *via* differential growth generally suggested that local populations were favored, however the patterns were not always clear. In some cases the patterns reversed between years. This is further evidence that acclimation was occurring for at least one and most probably two years after transplanting.

For the period from 1984 to 1986, selection clearly favored snowbed and fellfield ecotypes in their home sites *via* differential growth. Alien plants at fellfield and snowbed sites were decreasing in size (shoot number), while native

plants were maintaining their shoot population size near equilibrium (constant shoot numbers). If those trends were to continue, eventually alien individuals would begin to die. Thus, based on the present growth data, one could project further selection *via* differential survival against aliens at both sites. At the intermediate site, growth rates were identical among ecotypes, perhaps explaining why all three ecotypes are occasionally found there.

The direct measure of selection by differential fertility (flowering) was significant only in the last year of this study. This is evidence that even if ecotypes reach adult size in a foreign site, selection may reduce their contribution to the next generation. Such selection may be extremely strong in the case of alien snowbed and fellfield plants where transplanting to the opposite ends of the snowbank gradient reduced flowering to zero in both 1984 and 1986.

Long-term patterns of selection in *Dryas octopetala* ecotypes were different in rate and timing from the short-term patterns, however selection by differential survival continued to favor native ecotypes in snowbed and fellfield environments. In this respect, differential growth paralleled the patterns of survival, but a 1- or 2-year acclimation period was required before clear patterns emerged. The results for growth and survival emphasize the importance of making long-term observations in order to draw firm conclusions about a population-level response to the environment (Southern 1970).

Intermediate plants apparently did not represent a locally-adapted population (i.e., an ecotype) since their fitness was not greater than that of the other plants at the intermediate site. In terms of survival, the intermediates more closely resembled fellfield plants. In terms of growth, the response of intermediates varied, but from 1984-1986 their growth response fell between that of snowbed and fellfield plants at either end of the snowbank gradient; a further indication that intermediate plants were not members of a locally-adapted population. Naturally-established intermediates are probably first or second generation hybrids between fellfield and snowbed plants growing at or near the intermediate site. This speculation is consistent with Hulten's observations of "hybrid swarms" between *D. octopetala* ssp. *octopetala* (fellfield ecotype) and *D. octopetala* ssp. *alaskensis* (Hulten 1968). Their persistence in intermediate sites is probably due to the fact that they are not at a selective disadvantage there, although they are not at an advantage either. The lack of "perfect" adaptation, despite environmental differences, corroborates Schwagerle and Bazzaz's (1987) suggestion for differentiation in *Phlox* that there are limits to the power of selection in adapting local populations to their environment. For *Phlox* it was suggested that populations lacked the ability to adapt to small, multifactorial differences between sites. For *Dryas*, limits to adaptation are probably determined by the high rate of gene flow that has thus far prevented formation

of a third locally-adapted population along the snowbank gradient.

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