Educational Psychology: A Cognitive View by David P. Ausubel
Review by: Robert M. Gagné
American Educational Research Journal, Vol. 6, No. 2 (Mar., 1969), pp. 287-290
Published by: American Educational Research Association
Stable URL: http://www.jstor.org/stable/1161899
Accessed: 16/11/2011 18:10

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Journal of Ecology (1983), **71**, 879–897

EXPERIMENTAL ECOLOGY OF *DRYAS OCTOPETALA* ECOTYPES

I. ECOTYPIC DIFFERENTIATION AND LIFE-CYCLE STAGES OF SELECTION

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SUMMARY

(1) Natural populations of *Dryas octopetala* show large site-specific variations in phenotype. The genetic and environmental basis for this variation was examined in common-garden and reciprocal-transplant experiments. Morphological characters were examined in seedlings grown from seed in a 'common garden' in controlled growth chambers at the Duke University Phytotron. Adult plants of three *D. octopetala* populations were transplanted reciprocally at three sites along a snowbank gradient in mountains of interior Alaska.

(2) Several factors capable of maintaining genetic differentiation between adjacent snowbed and fellfield populations were studied. Restrictions on pollen flow by phenological and spatial isolation were determined. Barriers to gene flow, selection between ecotypes, and site effects within an ecotype were investigated experimentally by measuring survival of reciprocal transplants at the pollination, seed, seedling, and adult stages.

(3) Seedlings raised under common conditions showed differences in leaf size parallel to those observed in the field. Differences in leaf pubescence, used to distinguish two *D. octopetala* subspecies, were also maintained. The two most prevalent forms were therefore termed ecotypes.

(4) Leaf morphology was measured to assess phenotypic effects of reciprocal transplants of adults. Analysis of leaf traits suggested that greater morphological plasticity in the snowbed ecotype accounts for the bulk of the observed phenotypic differences between populations.

(5) Pollen flow was greatly reduced by separation of flowering times of the two ecotypes. More than 99% of pollen movement was between flowers of the same ecotype. Neither ecotype was apomictic or auto-fertile; both were self-incompatible. There were apparently no breeding system barriers to gene flow.

(6) Selection, measured as survival, favoured seedlings of the snowbed ecotype over those of the fellfield ecotype at the snowbed site (selection coefficient 0·55). At the fellfield site, selection favoured the fellfield ecotype at the adult stage (selection coefficient 0·50). No significant selection was demonstrated at any other life-cycle stage, although 10 of 11 stage-specific selection coefficients indicated a trend toward selection against an alien ecotype at both sites.

(7) Seed germination was higher and seedling survival lower at the fellfield site than at the snowbed site for both ecotypes. Therefore, the 'home' site was not always the 'better' site at all life-cycle stages; ecotypes were not perfectly matched with the environment. Therefore, selection at present acts only to give a relative advantage to native ecotypes.

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0022-0477/83/1100-0879 $02.00 © 1983 British Ecological Society

INTRODUCTION

The existence of habitat-associated races, or ecotypes, in plants is widespread (Turesson 1922; Clausen, Keck & Hiesey 1940, 1948; Clausen & Hiesey 1958); see Heslop-Harrison (1964) and Langlet (1971) for reviews. Nevertheless, the forces leading to habitat-specificity have most often remained unexplored. Genetic differentiation between adjacent populations has been recognized as a balance between gene flow and selection (Jain & Bradshaw 1966), and ecotypic differentiation over short distances may be similarly controlled. However, few realistic estimates of either selection or gene flow have been made in natural populations (Stearns 1976), and even fewer in populations that have not been disturbed by man.

Restriction of gene flow may occur before or after zygote formation—for examples, see McNaughton & Harper (1960); Levin & Kerster (1968) and Allard (1975). Selection may occur at pollination (de Nettancourt 1977), seed (Lindauer & Quinn 1972), seedling (Cavers & Harper 1967) and adult (Davies & Snaydon 1976) stages. However, these separate studies have not yielded overall measures of selection or gene flow. If gene flow and selection vary with life-cycle stage, their effects will be complex. For example, restrictions on pollen flow may act in parallel with limitations on seed dispersal, such that a strong restriction in one component of gene flow may have a reduced effect if the other is unrestricted.

The net effect of selection at different life-cycle stages is a multiplicative function of the intensity of selection at each of several stages and the duration of each stage. Effects at different stages may offset or augment those at others. The significance of selection at any one stage, therefore, can be determined only in the context of the entire life cycle.

In this paper, we first demonstrate the existence of ecotypes (*sensu* Turesson 1922) in *Dryas octopetala* L. (Rosaceae). In alpine areas of interior Alaska, *D. octopetala* varies greatly between adjacent populations. A small, mat-forming dwarf shrub form is common in severe ridge-top environments, while a larger-leaved, prostrate shrub form is most abundant in the lee of ridges in areas of late-lying snow. The two phenotypes are often found growing in nearly pure stands only metres apart.

The second objective of this paper was to examine simultaneously factors known to contribute to population differentiation. These included effects of breeding system, phenological isolation, and isolation by distance on gene flow, as well as selection at the pollination, seed, seedling, and adult stages as demonstrated with experimental transplants. We asked three questions: (i) is differentiation the product of several interacting factors operating at different life-cycle stages, or is one factor more prominent than all others; (ii) does selection always favour an ecotype in its native habitat or do the different stages of selection oppose each other; and (iii) does an ecotype always have a greater survival rate in its home environment than in a foreign environment?

METHODS

Plant materials

Variation within the genus *Dryas* has been studied by Juzepczuk (1929), Hultén (1959), and Elkington (1965). Three species were recognized by Hultén (1959): *Dryas drummondii*, *D. integrifolia*, and *D. octopetala*. All are found in Alaskan tundra. *Dryas octopetala* contains two extreme forms (Fig. 1), designated subspecies by Hultén (1959) on the basis of pubescence and gland characters, and on the the relative rarity of

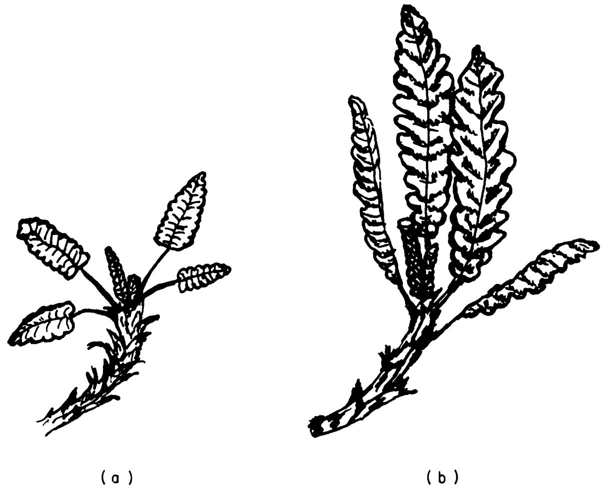

FIG. 1. Single shoots of *Dryas octopetala* (a) from a fellfield site (ssp. *octopetala*) and (b) from a snowbed site (ssp. *alaskensis*) in interior Alaska.

intermediates. A circumpolar form, ssp. *octopetala*, has small (5–15 mm) deciduous leaves (Fig. 1(a)) and commonly lives more than 100 years (Kihlman 1980). It is found on exposed alpine ridges, often in nearly pure stands. The opposite extreme, ssp. *alaskensis*, probably evolved from ssp. *octopetala* in Alaska during the Pleistocene (Hultén 1959); it has large (15–50 mm) evergreen leaves (Fig. 1(b)) and a more extensive clonal growth pattern. Present in several vegetation types, it reaches peak abundance in snowbeds (Gjaerevoll 1980). Individuals of both subspecies form prostrate mats of shoots connected by woody stems. While intermediates between these two forms are not as common as either extreme, hybrid swarms are observed in the field (Hultén 1968). These hybrid swarms often occur in intermediate habitats and are phenotypically intermediate between ssp. *alaskensis* and ssp. *octopetala*.

Field site

Field studies were carried out near Eagle Summit at mile 106 on the Steese Highway in an unnamed interior Alaskan mountain range (65°26′N, 145°30′W; altitude 1050 m). The study site was a snow-free ridge-top sloping to a snow accumulation area in the lee of the ridge (the snowbed) and wet tundra below the snowbed. Such a gradient is frequent on Alaskan interior mountains, and distinct vegetation types (Fig. 2) are associated with it (Oberbauer & Miller 1979). The gradient at the study site spanned 150 m from the top of the ridge to the wet tundra community, dropping approximately 30 m over this distance. A depression in the centre of the gradient consistently accumulated snow to more than 3·5 m before melting began in May. The shape and rate of recession of the snowbank are shown in Fig. 2 for 1981, a typical year. Correspondence of the spatial distribution of snow with vegetation zones (Fig. 2) suggests that winter exposure, growing season length, and other factors affected by snow accumulation, are important in determining vegetation type (Miller 1982). Nutrient availability, vascular plant cover and biomass are higher and the growing season is shorter in the snowbed than on the fellfield (Miller 1982). Moisture availability is generally adequate except in the *Cassiope*-grass zone where short drought periods may occur (Oberbauer & Miller 1979).

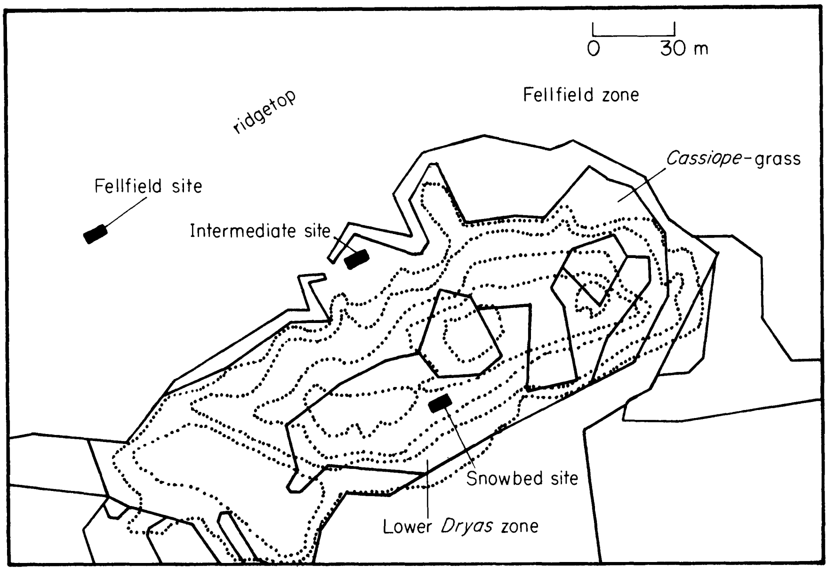

FIG. 2. Boundaries of several vegetation types (solid lines) at the Eagle Summit, Alaska, study area, classified according to Oberbauer & Miller (1979); only fellfield, lower *Dryas* and *Cassiope*-grass zones are identified here. Dotted lines show the position of the snowbank edge at weekly intervals in 1981, that of greatest extent was on 15 May.

Dryas octopetala ssp. *octopetala*, distinguished by 'octopetala scales' on the abaxial leaf surface (Hultén 1959), predominates in the fellfield vegetation, whereas ssp. *alaskensis*, with stalked glands on the mid-vein of the abaxial leaf surface, is the dominant vascular plant species in the lower *Dryas* zone. A map of maximum leaf lengths, superimposed on the subspecies distribution, shows the continuous variation in this trait (Fig. 3).

Common-garden experiment

Seeds were collected from fellfield ssp. *octopetala* and snowbed ssp. *alaskensis* in mid-August 1980, and frozen at −17 °C. On 25 and 26 September 1980, full-seed batches capable of greater than 95% germination (McGraw 1982) were placed on moist filter paper in plastic petri dishes under a 16 °C by day, 4 °C by night temperature regime (20-hour photoperiod, 300 μEinstein m^{-2} s^{-1}). Germination began on 1 October and continued for several days. On 8 October, 350 seedlings of each subspecies were planted in 'Turface' (an arcillite clay plant-growth medium, prepared by International Minerals Corporation) and placed in a growth chamber. Seedlings were watered twice daily with distilled water and given half strength Hoagland's solution twice weekly. The irradiance, measured at plant level with a Li-Cor quantum sensor, was 750 μEinstein m^{-2} s^{-1}. The photoperiod in the chambers was adjusted monthly to simulate a natural growing season beginning in early June. Twenty, 18-, and 16-hour photoperiods corresponded approximately with late June, July and early August conditions at the Eagle Summit site. Temperatures were also adjusted monthly as follows: June, 13 °C by day, 2 °C by night; July, 16 °C by day, 4 °C by night; August, 10 °C by day, −1 °C by night. After 70 days, total leaf number, shoot number, and lengths of the longest leaf were determined.

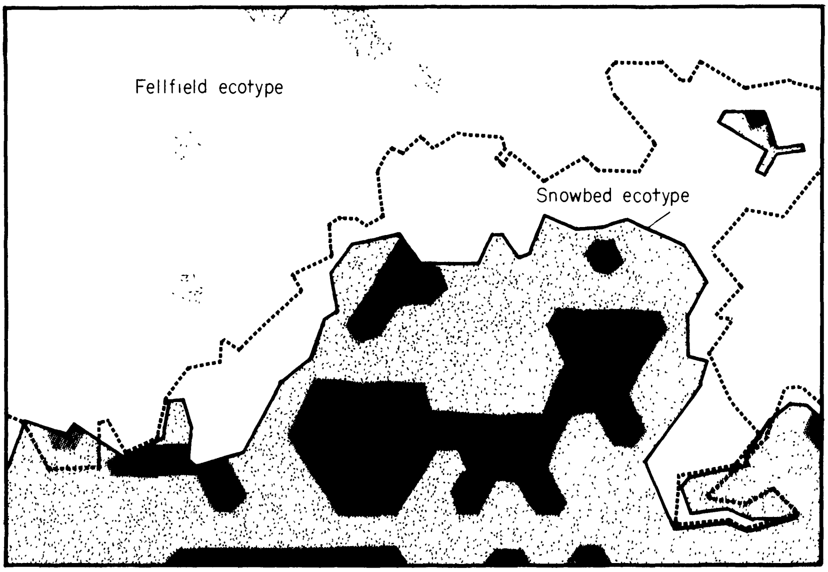

FIG. 3. Map of the distribution of *Dryas octopetala* subspecies according to leaf-gland and scale characters. Shaded areas show the cline in leaf lengths of *D. octopetala* across the study area at Eagle Summit, Alaska. Mean maximum leaf lengths were measured for ten randomly-chosen shoots in 2 × 2 m quadrats at 15 m intervals across the study area. Unshaded area, <20 mm; lightly shaded, 20 to 30 mm; heavily shaded, >30 mm.

Reciprocal transplants

Three *D. octopetala* populations were sampled from three large vegetation zones on the ridge and snowbank gradient. Plants at the two extreme sites corresponded to ssp. *octopetala* and ssp. *alaskensis*. Plants at an intermediate site, distinguished by intermediate leaf size, were also sampled. Transplanting the intermediate forms allowed a determination of whether they were also genetically intermediate between the two extreme *D. octopetala* forms.

In late July 1979, ten adult plants from each population were transplanted to each of the three experimental sites in the fellfield, *Cassiope*-grass, and lower *Dryas* zones (shown in Fig. 2). Some soil was transferred with the plants to minimize root damage. It was not possible to insert transplants without disrupting the surrounding vegetation. Therefore, a standard zone 2–4 cm in width was cleared around each individual transplant. Outside this zone, the vegetation was undisturbed. Transplants were watered once and then allowed to become established.

On 14 August 1981, after 2 years of acclimatization to transplant sites, ten replicate leaves were collected from four individuals (three leaves from two individuals and two leaves from the remaining individuals) in each transplanted population. The following were measured: petiole length (distance from stipule to the base of the leaf blade); number of teeth; blade length; width at widest point between teeth (minimum width); width at the widest point including teeth (maximum width); dry weight; and leaf area. Leaf area was determined by tracing leaves and weighing the paper image. Additionally, the number of teeth per unit length, the degree of leaf dissection (maximum width divided by minimum width) and the specific leaf weight (leaf weight per unit area) were determined. Results from the ten leaves sampled from each population at each site were pooled and therefore between-genotype variance was not estimated in analysis of variance.

In 1981, several taxonomic characters were determined for a random sample of three individuals in each population at each site, including presence or absence of abaxial and adaxial leaf pubescence, viscid glands, and stalked hairs or 'octopetala scales' (Hultén 1968). All leaves were produced *in situ* and therefore should reveal any site-induced morphological changes.

Pre-zygotic barriers: breeding system

In June 1979, the breeding systems of fellfield and snowbed populations of *Dryas octopetala* were examined. Bags were placed over 125 flowers immediately prior to anthesis. Twenty-five flowers were emasculated and hand-pollinated with pollen from the same population and twenty-five were emasculated and hand-pollinated with pollen from the other population. In addition, manipulations were made to determine the extent of apomixis (emasculated, no pollen transferred), auto-fertility (not emasculated, no pollen transferred), and self-fertility (not emasculated, own pollen transferred by hand), with twenty-five replicates per manipulation. After petals abscised and stigmas were no longer receptive (between 5 and 10 days after bagging), the bags were removed and the seeds were allowed to develop. Seeds were collected in August when the seed coat dried and the seeds began to loosen from the flower receptacle. Numbers of full seeds were determined with a dissecting microscope. A separate trial showed that more than 95% of the seeds classified as 'full' were capable of germination.

Pre-zygotic barriers: pollen dispersal

The onset of the growing and flowering seasons for snowbed plants ranges from 0 to 2 months later than for fellfield plants (see Fig. 2). A second obvious effect of the two different environments is that of the distance between them. The precise effects of distance are unknown in the absence of extensive pollinator data but *D. octopetala* is insect-pollinated (Hocking & Sharplin 1965).

The effects of flowering time and distance on isolation were studied in the 6·24 ha (208 × 300 m) area covered by Fig. 2 with adjacent fellfield and snowbed *D. octopetala* populations. The area was staked out in a hexagonal grid. Each stake within the borders of the study area was 15 m from six neighbouring stakes. During the 1981 flowering season (3 June–12 July), daily counts of all *D. octopetala* flowers were made in a 2 × 2 m quadrat (with the stake at the centre of the quadrat) for each stake in the grid (357 stakes). Flowers were identified as fellfield or snowbed forms using established taxonomic criteria (Hultén 1968). Intermediates, though identified and counted, were not included in the analysis; their flowers comprised less than 1% of the total flowers counted.

Daily flowering data were used to determine the fraction of total possible pollinator paths (to all flowers of *Dryas octopetala*) leading to flowers of the same subspecies population. This fraction was calculated for both populations on each day of the flowering season to determine the time-course of potential between-population pollinations, as well as for the entire season. At first no distance weighting of paths was made, to determine the sole effect of flowering phenology differences. We assumed (conservatively) that no flower could act as a pollen source for another flower in the same quadrat.

A similar fraction was calculated as an estimate of distance effects; this was the fraction of possible pollinator paths 15 m in length leading to flowers in the same subspecies population. This is probably a conservative index of distance effects in that it assumes that every pollinator moves 15 m before transferring pollen. As a check that 15 m was a conservatively long pollinator flight, pollinators (primarily flies) were observed on 2 July 1980. The weather was clear and warm and a single flight distance was measured for each pollinator.

Selection

Intensities of selection were estimated from reciprocal transplant experiments for four stages of the plant life cycle. Pollen, seeds, seedlings, and adults from fellfield and snowbed populations were transplanted in 'home' and 'foreign' environments.

The 'home' and 'foreign' environments for pollen transplants corresponded with the stigmas of the native and alien plants, respectively. Success of pollen transplants was measured in terms of production of full seed. Seed transplants were carried out on 10 June 1981. Four hundred full seeds from each of the fellfield and snowbed populations were taken at random from seed heads collected in 1980 which had been stored during the winter at −17 °C. Seeds from both populations were sown in lots of twenty at ten random locations in a 5 × 5 m grid in both fellfield and snowbed sites. Nylon netting was pinned to the soil over each seed lot. The mesh of the netting was fine enough (*c.* 4 mm) to prevent seeds from being blown away, but large enough to allow germination of seeds and growth of seedlings. Surrounding plants were removed to provide a 2-cm 'buffer zone' around each seed lot. The success of the transplants was measured by counting germinated seeds. A seed was considered to have germinated when the cotyledons emerged from the seed coat.

Seedling transplants were performed with a modified phytometer technique (Antonovics & Primack 1982). Between 18 and 25 June 1980, 200 soil cores (twenty per block in ten randomly located blocks per site) were extracted with a 5·4 mm diameter cork borer in each of the fellfield and snowbed sites. To preserve the shape of the hole from which the soil core was taken and to preserve the water balance of the surrounding soil, a 4-cm hollow plastic tube of the same diameter as the soil core, was placed in the hole. Each soil core, ranging in depth from 0·5 cm to 2·5 cm, was then injected into a 3-cm plastic tube of the same diameter. One hundred full seeds from each population were planted individually in soil cores assigned randomly from each site. The seeds and soil were kept moist with a hand-held mist sprayer. The seeds germinated within 2 weeks, and all the seedlings were raised until at least one leaf protruded beyond the cotyledons. No consistent differences in size between subspecies populations were observable at that stage. In mid-July, the seedlings were returned to the field. Each soil core was placed in the hole from which it was originally extracted and the plastic tubes were removed. The microhabitat of the seedling was therefore undisturbed except that it was necessary to remove the surrounding vegetation to a distance of 2 cm to facilitate the removal of the soil plug and the implanting of the seedling. Seedlings were counted in August 1980 and in May and August of 1981. Survival of seedlings was estimated for the periods between censuses and over the entire year.

The success of mature *D. octopetala* plants as a function of site was measured by the adult reciprocal transplants (described above). The survival from August 1979 to August 1981 was determined for fellfield and snowbed plants transplanted to home and foreign sites.

RESULTS

Common-environment experiment

Seventy-day-old seedlings grown under uniform phytotron conditions showed population differences parallel to those observed in the field. The numbers of meristems and leaves were not significantly different between the populations despite a large sample size, but the maximum leaf length was greater in the snowbed plants (6·68 ± 0·14 mm (S.E.)) than in fellfield plants (4·70 ± 0·10 mm), although plants were still immature after 70 days. The leaves of the fellfield seedlings had fine silvery hairs, while snowbed seedlings were glabrous for the period of observation.

Reciprocal-transplant experiment

Several of the measured leaf attributes were correlated (Table 1). In particular, leaf dimensions were highly correlated (Pearson product-moment correlation coefficient, $r > 0{\cdot}65$). The teeth per unit length was negatively correlated with all the other characters.

TABLE 1. Pearson product-moment correlation coefficients for ten *Dryas octopetala* leaf characters. Leaves of plants in a reciprocal transplant experiment carried out in Alaska were used in the analysis. Data for all ecotypes were pooled. ($n = 90$).

	Petiole length	Teeth (number)	Length	Minimum width	Maximum width	Leaf weight	Leaf area	Teeth per mm	Dissection
Teeth (number)	0·53								
Length	0·75	0·72							
Minimum width	0·63	0·42	0·66						
Maximum width	0·67	0·53	0·82	0·81					
Leaf weight	0·74	0·64	0·93	0·68	0·86				
Leaf area	0·74	0·63	0·93	0·76	0·89	0·96			
Teeth per mm	−0·62	−0·25	−0·79	−0·67	−0·75	−0·71	−0·74		
Dissection	−0·22	0·27	−0·42	0·06	−0·51	−0·44	−0·39	0·34	
Specific leaf weight	0·31	0·38	0·48	0·18	0·37	0·56	0·34	0·33	−0·31

A two-way analysis of variance revealed a highly significant main effect of population on all ten leaf characters measured ($P < 0{\cdot}01$). Transplant site also exhibited a strong effect on every character ($P < 0{\cdot}01$) except number of teeth. A significant population-site interaction was demonstrated in every character ($P < 0{\cdot}05$) except leaf dissection. This interaction indicated that the response to the environment differed among populations along the transect. A two-way analysis of variance on logarithmic or arcsine-square root transformed data yielded equivalent significance levels and did not eliminate the interaction effects. Overall, population, site, and population-site interactions were able to explain a large amount of the variance in leaf traits ($0{\cdot}39 < r^2 < 0{\cdot}73$).

The snowbed plants, when transplanted to the fellfield site, became smaller in every leaf dimension measured (Table 2). The number of teeth changed little and the leaves had a stunted appearance. The degree of leaf dissection remained fixed on the fellfield site and specific leaf weight declined.

The fellfield plants, grown in the snowbed site, showed fewer changes in the foreign environment (Table 2), but where change did occur it was in the direction of increasing resemblance to snowbed plants. Blade length, leaf width, leaf weight, and leaf area all increased in the snowbed site. Teeth per unit length declined, specific leaf weight was unchanged, and the degree of leaf dissection increased in the snowbed site.

TABLE 2. Mean values of some leaf traits of reciprocally-transplanted individuals of subspecies and intermediate populations of *Dryas octopetala* in interior Alaska. Means which are not significantly different are labelled with the same letter among populations within sites (next to mean), and among sites within populations (line below mean). FF: fellfield population; INT: intermediate population; SN: snowbed population.

Site	Fellfield			Intermediate			Snowbed		
Population	FF	INT	SN	FF	INT	SN	FF	INT	SN
Petiole length (mm)	3·18a	4·83b	3·45a	3·11a	5·20b	7·45c	3·15a	4·20a	6·25b
	a	a	a	a	a	b	a	a	b
Teeth per leaf	8·10a	8·30a	9·30a	7·56a	10·20b	10·60b	7·60a	8·20a	10·80b
	a	a	a	a	b	a	a	a	a
Blade length (mm)	7·93a	11·15b	10·18b	7·28a	13·30b	20·45c	9·80a	11·90a	18·40b
	a	a	a	a	a	b	b	a	b
Minimum width (mm)	2·83a	3·65b	2·55a	2·58a	4·00b	4·30b	3·50a	3·45a	3·55a
	a	a	a	a	a	b	a	a	c
Maximum width (mm)	3·75a	5·05b	5·05b	3·44a	5·45b	7·45c	5·25a	5·35ab	6·55b
	a	a	a	a	a	b	b	a	ab
Leaf weight (mg)	2·49a	4·87b	4·56b	2·12a	7·61b	14·99c	4·57a	5·40a	12·73b
	a	a	a	a	b	b	b	ab	b
Leaf area (cm^2)	0·27a	0·54b	0·46b	0·25a	0·65b	1·27c	0·44a	0·56a	0·97b
	a	a	a	a	a	b	b	a	b
Teeth (mm^{-1})	1·04a	0·75b	0·95a	1·07a	0·77b	0·53c	0·77a	0·70ab	0·61b
	a	a	a	a	a	b	b	a	b
Dissection (maximum width/minimum width)	1·33a	1·39a	1·92b	1·32a	1·35a	1·75b	1·52a	1·54a	1·79b
	a	a	a	a	a	a	b	b	a
Specific leaf weight (mg cm^{-2})	9·23a	9·38a	9·56a	8·98a	12·01b	11·87b	10·47a	9·51a	12·96b
	a	a	a	a	b	b	a	a	b

Environmental effects on intermediate plants were less pronounced than for either extreme form. No leaf dimensions changed significantly, but the number of teeth and specific leaf weights decreased in the foreign fellfield and snowbed sites. The degree of leaf dissection increased in the snowbed environment.

The leaf pubescence characters, used to distinguish the fellfield and snowbed forms taxonomically (Hultén 1959), were unaffected by reciprocal transplanting. The abaxial orange scales and branched hairs distinguished leaves of the fellfield form in all sites. The abaxial glands were a constant character in the snowbed forms. Resin exudates found naturally on the snowbed form growing in the snowbed were not produced on the fellfield. Intermediates possessed orange 'octopetala scales' characteristic of the fellfield form. Some intermediate plants also possessed glands like those found in the snowbed form.

Phenotypic differences among populations may result from direct environmental effects and genetic differences. In the simplest case (Fig. 4(a)), the phenotypic responses to reciprocal transplants for two populations are parallel. The phenotype may be fixed ($\Delta e = 0$), partly affected (shown), or completely changed ($\Delta g = 0$) to resemble the population at the opposite end of the gradient. These three possible responses correspond to irreversible genetic differentiation, some plasticity and some irreversible differentiation, and complete plasticity, respectively. For most *D. octopetala* leaf characters the responses were not parallel (Fig. 4(a–c)), although the genetic component of change was always in the same direction as the clinal change (i.e. there has been 'cogradient selection', *sensu* Berven, Gill & Smith-Gill 1979). In general, the fellfield form of *D. octopetala* changed less than the snowbed form.

Three permutations of change in leaf characters were shown by *D. octopetala*. The petiole length was a completely plastic character in the snowbed plants, but had no environmental component in fellfield plants (Fig. 4(b)). The specific leaf weight was also

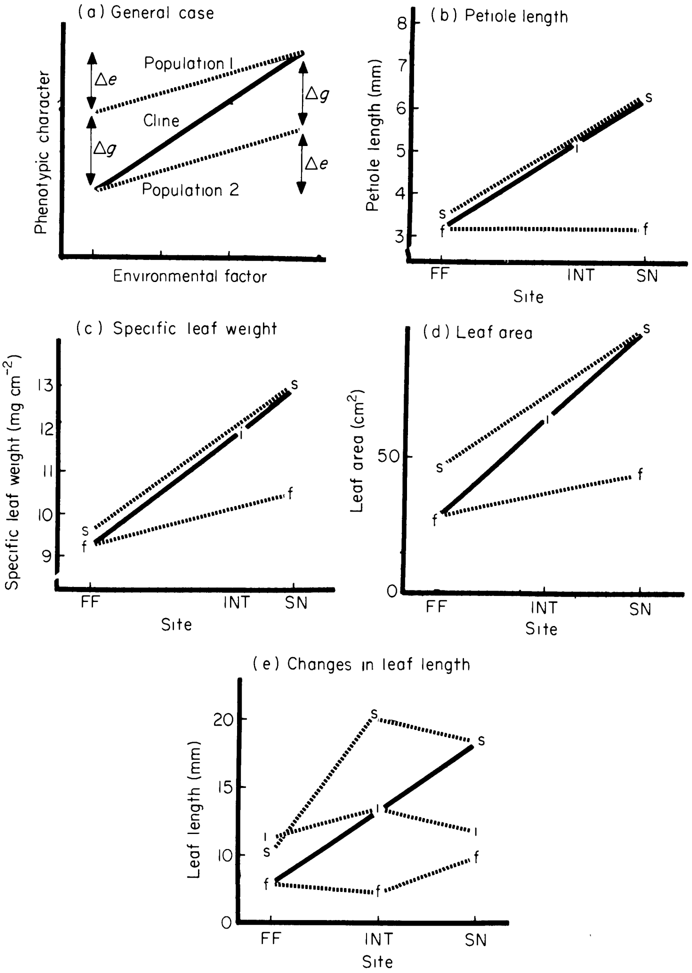

FIG. 4. Effects of environment and genotype on plants from reciprocally transplanted populations. (a) shows a general case, where *e* is the change in phenotype induced by the environment with transplanting and *g* is the unalterable component, determined genetically. (b–d) changes in (b) petiole length, (c) specific leaf weight, and (d) leaf area in transplanted populations of *Dryas octopetala* in a snowbank gradient in Alaska; s indicates the population originally from the snowbed, and f that from the fellfield. The phenotypic position of intermediates along the cline is indicated by i. (e) changes in leaf length in reciprocal transplants of the snowbed, fellfield and intermediate populations of *Dryas octopetala*.

completely plastic in the snowbed form while the fellfield form showed some genetic and some environmental control (Fig. 4(c)). In both populations, leaf area was controlled by both environmental and genetic factors (Fig. 4(d)).

The phenotypic response to transplanting was not linear along the snowbank gradient. The intermediate site did not produce a phenotype intermediate between that found at the two extreme sites (Fig. 4(e)). Leaf lengths of snowbed and fellfield plants were not significantly affected by the intermediate environment.

Since growth under constant conditions and reciprocal transplant studies revealed a partial genetic basis for the phenotypic differences between fellfield and snowbed forms, these populations will henceforth be termed ecotypes (*sensu* Turesson 1922).

Breeding system

Dyras octopetala populations at Eagle Summit showed no apomixis, auto-fertility, or self-fertility. The results of crosses between ecotypes were inconclusive. Flowers of the fellfield and snowbed ecotypes produced means of 13·4 and 19·7 seeds, respectively, when fertilized with pollen from the snowbed. When pollen from the fellfield plants was transferred to stigmas of fellfield and snowbed plants, means of 17·7 and 8·0 seeds per flower were produced, respectively. The means were not significantly different at $P = 0{\cdot}05$, although there was a trend (*t*-test, $P = 0{\cdot}07$) toward partial incompatibility of fellfield ecotype pollen with snowbed ecotype ovules. The crosses were repeated in the field in 1981 to verify this trend, but no crosses were successful owing to unusually low temperatures (McGraw, Stuart & Chester 1983) during seed maturation.

Pollen dispersal

Flowering in the snowbed ecotype was delayed and extended relative to that of fellfield plants (Fig. 5), particularly in areas of late-lying snow. For fellfield plants, this meant that the potential for pollen dispersal was primarily within the population during peak flowering season (Fig. 6(a)). Over the entire season, 80% of potential pollinator flight paths led to flowers of the same ecotype. If the same index is calculated only for plants 15 m from the pollen source (Fig. 6(b)), gene flow was potentially 99·5% within the population over the whole flowering season.

For the snowbed ecotype, there were fewer total flower-days and a substantial proportion of flowering occurred during peak flowering of the fellfield ecotype (Fig. 5). This pattern meant that while the fraction of potential pollinator paths within the population mirrored that for fellfield plants through the season (Fig. 6(a)), between-population crosses were potentially frequent early in its peak flowering period. Over the entire season, 53% of the potential pollinator paths were within the snowbed population. Inclusion in the calculation of only those plants 15 m from the pollen source (Fig. 6(b)) sharply reduced the frequency of between-population pollinator paths, resulting in a seasonal within-ecotype pollination potential of 99·3%.

Observations of twenty pollinator flights gave a mean flight distance of 0·44 m with a leptokurtic frequency distribution. Only three flights were greater than 1 m and none were

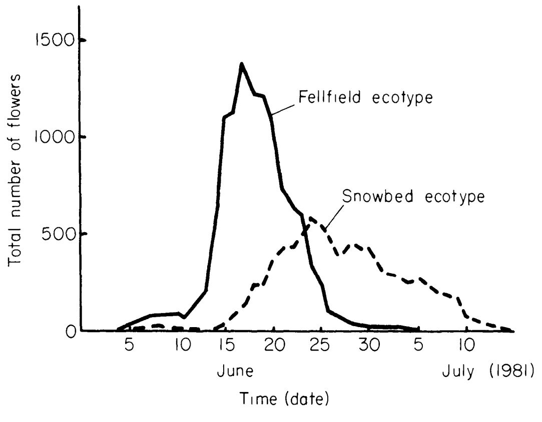

FIG. 5. Number of flowers of snowbed and fellfield ecotypes of *Dryas octopetala* produced in a total of 357 2 × 2 m quadrats in 1981 near Eagle Summit, Alaska.

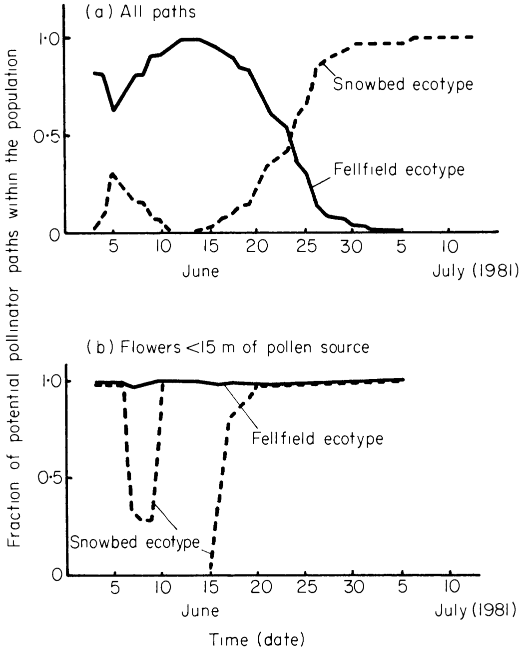

FIG. 6. Fraction of potential pollinator paths leading to flowers of the same ecotype population of *Dryas octopetala* at Eagle Summit, Alaska. Fractions were calculated as (number of paths leading from all flowers of an ecotype to flowers of the same ecotype)/(total number of paths leading from all flowers of an ecotype to all flowers of *D. octopetala*). (a) shows data for all paths irrespective of distance between flowers; (b) shows the same fraction for flowers within 15 m of the pollen source.

more than 3 m. The isolation effect estimated by assuming 15-m flights was therefore probably conservative.

Seed transplants

Full seeds germinate readily when sown on moist filter paper in growth chambers. However, a maximum of 7% germination was recorded for comparable field-sown seeds subject to natural conditions (Table 3). No ecotypic differences could be established in germination, but the fellfield was a better germination environment than the snowbed (two-way analysis of variance, $P < 0{\cdot}05$).

Seedling transplants

Winter survival of seedlings was much lower on the fellfield than in the snowbed (Duncan's multiple range test, $P < 0{\cdot}05$) (Table 3). During winter, neither ecotype was favoured in either environment. In summer, however, snowbed plants survived significantly better than fellfield plants in the snowbed site (t-test, $P < 0{\cdot}01$). Survival over the entire year from August 1980 to August 1981 was greater in the snowbed than in the fellfield (two-way analysis of variance, $P < 0{\cdot}0001$), and snowbed plants survived at a higher rate than fellfield plants at the snowbed site (t-test, $P < 0{\cdot}01$).

TABLE 3. Mean proportions of seeds germinating, seedlings surviving (through their first winter, subsequent summer, and to 1 year), and adults surviving (2 years) for *Dryas octopetala* ecotypes transplanted reciprocally to home and foreign sites (fellfield and snowbed) in Alaska. Sample size in parentheses.

		Transplant site	
Stage	Ecotype	Fellfield	Snowbed
Seed	Fellfield	0·07 (200)	0·01 (200)
	Snowbed	0·04 (200)	0·02 (200)
Seedling			
Winter	Fellfield	0·08 (39)	0·70 (34)
	Snowbed	0·09 (47)	0·79 (34)
Summer	Fellfield	0·67 (3)	0·50 (24)
	Snowbed	0·25 (4)	0·96 (27)
1 year	Fellfield	0·05 (39)	0·34 (34)
	Snowbed	0·02 (47)	0·77 (34)
Adult (2 years)	Fellfield	1·00 (10)	1·00 (10)
	Snowbed	0·50 (10)	1·00 (10)

Adult transplants

The fellfield ecotype survived equally well (100%) in the snowbed and fellfield sites (Table 3). However, 2-year survival of the snowbed ecotype was significantly reduced on the fellfield (Fisher's exact test, $P = 0{\cdot}016$).

DISCUSSION

The difference in leaf size observed between phytotron-grown seedlings of the fellfield and snowbed ecotypes reflects what is obvious in the field, and must result partly from genetic differences. However, this assumes that the phytotron-grown plants were not affected by differential seed size effects (or other 'maternal' effects) and that the seeds were formed by mating within populations. The first assumption is probably valid as no difference between ecotypes in seed weight was found (McGraw 1982). The second assumption is supported by the low overlap in flowering phenology.

Reciprocal transplants of adults show what proportion of the phenotypic difference between ecotypes in native sites is due to site effects and to genetic differentiation. For *D. octopetala* leaf characters it may also be possible to infer the course of past evolution. If, as biogeographical evidence suggests, the snowbed ecotype evolved from the fellfield form (Hultén 1959), this evolution involved increased plasticity in response to snowbed conditions. Thus, though the snowbed environment produced long petioles, large leaf size, many teeth, and a high specific leaf weight in the snowbed ecotype, it did not do so with fellfield plants. Plasticity varied from trait to trait. Only in snowbed plants was petiole length potentially variable, but for specific leaf weight, some plasticity existed in fellfield plants, and more has evolved in the snowbed ecotype. In leaf area, and all correlated leaf size measures, there was originally some plasticity, and more has evolved, but a non-plastic component has evolved as well. All of these arguments assume that the progenitor of the snowbed ecotype resembled the present-day fellfield ecotype, for which there is macrofossil and biogeographical evidence (Hultén 1959; Elkington 1971).

Genetic differentiation between fellfield and snowbed ecotypes extended beyond a contrasting level of plasticity. Responses of the ecotypes to the intermediate site, for example, differed not only in amount, but in direction. For most characters, the snowbed ecotype produced leaves resembling those grown in the snowbed. On the other hand, the fellfield ecotype responded to the intermediate environment with leaves like those grown on the fellfield. Clearly, the environmental gradient from the snowbed to the fellfield was not a simple, linear gradient in a single factor to which morphological characters responded in a linear manner. The term ecotype now means more than simple habitat-correlation of races (Heslop-Harrison 1964; Langlet 1971). Current use of the term assumes, often without experimental justification, that the observed correlation was established by differentiation of ecologically important traits.

Temporal and spatial isolation of flowering are known to contribute to differentiation between adjacent populations and even adjacent plants (McNeilly & Antonovics 1968; Levin & Kerster 1968; Schaal 1980). Both factors were potentially important in the maintenance of ecotypic differentiation in *D. octopetala.* Data on pollen dispersal should be interpreted with caution, however. Flower phenology data from only 1 year may not be respresentative and, without measures of pollen movement, the effect of distance on isolation is uncertain. Pollinator flight distance may be an underestimate of pollen dispersal since carryover of pollen may occur. In insect-pollinated *Lupinus texensis* (Schaal 1980) maximal pollen movement is twice the pollinator flight distance. Our estimate of distance effects based on pollen dispersal of 15 m therefore was still probably conservative. Some long-range pollen flow may have occurred, but differences in flowering time would reduce its effectiveness.

Seed dispersal was not examined, but it may be important in gene flow in the field. The light seeds of *Dryas octopetala* are tipped by feathery styles which are probably an adaptation for wind-dispersal. In August, seeds are frequently loosened and dispersed during high winds which are sometimes greater than 100 km h^{-1} on the fellfield site. At the time of dispersal, seed heads are generally less than 20 cm above the soil surface and, therefore, the distance a seed travels before landing may be short even with secondary movements under windy conditions. Fellfield wind speeds were consistently higher than those in the snowbed only 100 m away, so that seed dispersal between the sites would not be equal; a fellfield seed is much more likely to be dispersed to the snowbed that vice versa.

Apomixis, auto-fertility, or self-fertility would reduce mating between genotypes or populations (Allard 1975). The lack of evidence for these features in the breeding system of either ecotype suggests that the breeding system *per se* did not serve to restrict pollen flow.

To estimate selection intensities, we calculated a selection coefficient for each life-cycle stage as follows:

$$\text{selection coefficient} = 1 - \left(\frac{\text{survival of a given ecotype}}{\text{survival of best-growing ecotype}}\right)$$

This coefficient differs from that used by previous authors (Jain & Bradshaw 1966; Davies & Snaydon 1976; Lovett Doust 1981) in that it does not assume that the native ecotype is

TABLE 4. Stage-specific selection coefficients (defined in text) for ecotypes of *Dryas octopetala* transplanted into alien and home sites in Alaska. Significance levels are calculated from comparisons of means of data in Table 3 by t-test or (in the case of adults), by a test of equality of two percentages and refer to differences from a selection coefficient of 0 (no selection). Symbols: * $P < 0{\cdot}05$; ** $P < 0{\cdot}01$; *** $P < 0{\cdot}001$; $^{\mathrm{NS}}$ not significant.

		Pollination	Seed	Seedling survival			Adult
Site	Ecotype	success	germination	Winter	Summer	1 year	survival
Fellfield	Fellfield	0	0	0·11$^{\mathrm{NS}}$	0	0	0
	Snowbed	0·24$^{\mathrm{NS}}$	0·38$^{\mathrm{NS}}$	0	0·63$^{\mathrm{NS}}$	0·57$^{\mathrm{NS}}$	0·50**
Snowbed	Fellfield	0·59$^{\mathrm{NS}}$	0·33$^{\mathrm{NS}}$	0·14$^{\mathrm{NS}}$	0·48**	0·55**	0
	Snowbed	0	0	0	0	0	0

the most successful ecotype. A selection coefficient of 0 indicates that an ecotype is the most successful ecotype, while a coefficient of 1 indicates complete selection against an ecotype.

Strong selection was observed against fellfield ecotype seedlings in the snowbed and against adult snowbed plants on the fellfield (Table 4). While only two selection coefficients were significantly different from zero, 10 of 11 coefficients indicated selection against the alien ecotype. Therefore, a strong possibility exists for the multiplicative action of stage-specific selection. Overall selection may thus be even stronger than the 0·50 and 0·55 values estimated from significant differences at one stage. Nevertheless, the measured selection against seedlings was probably sufficient to account for the rarity of fellfield plants in the snowbed. Models of genetic differentiation between adjacent populations predict that a steep gradient in gene frequencies will develop under such selection, even with high rates of gene exchange (Jain & Bradshaw 1966). The measured selection against adults of the snowbed ecotype may also account for its distribution.

Separation of selection into different life-history components has been carried out in an experimental population of the annual *Hordeum vulgare* L. by Clegg, Kahler & Allard (1978). They found that measures of overall selection underestimate the fraction of the reproductive potential of a population that is lost in differential mortality. This underestimate, in turn, has consequences for arguments concerning genetic load and maintenance of genetic variability in a population. These matters are likely to be even more important in long-lived perennial plants in which certain life-history stages are exposed to selection for a long time.

The assumption that certain traits are adaptations is dangerous in the absence of data showing selective advantage for them (Antonovics & Primack 1982). This is also true if selection is known to occur, but its effects at critical life-cycle stages are not known; in this case, an adult trait may be interpreted as adaptive when in fact selection occurs primarily at the seed or seedling stage. Seeking the adaptation at the adult stage would lead to entirely specious 'adaptive storytelling' (Gould & Lewontin 1979). That stage-specific effects are important is not new (Sagar & Harper 1961), but this is emphasized in a genetic context by our findings that an early stage (seedling) may indeed adequately account for selection against the fellfield ecotype in the snowbed environment.

A related argument for examining life-cycle stages is that even if selection is demonstrated at one stage, the net effect on fitness is unknown. Several studies have demonstrated selective advantages at various life-cycle stages under field conditions: seeds—Lindauer & Quinn (1972); seedlings—Cavers & Harper (1967); adults—Davies

& Snaydon (1976). All else being equal, these advantages should translate into effects on fitness. The few studies of natural populations which have examined more than one stage in a life cycle have suggested that it was important to do so (Cavers & Harper 1967; Clegg & Allard 1973; Clegg, Kahler & Allard 1978; Silvertown 1981). One study (Clegg, Kahler & Allard 1978) even suggested that the different stages of selection were opposed to each other. The data presented here do not indicate an opposition of selective forces at different stages, as only one stage was demonstrated to be significant in each site. However, if any trend exists, it is toward consistent selection in favour of the native ecotype at all life-cycle stages, as suggested above.

In addition to their use as tools for measuring selection intensities, reciprocal transplants have been used as measures of the environment, or phytometers (Antonovics & Primack 1982). We can therefore define a quantity termed the environmental discrimination coefficient as follows:

Environmental discrimination coefficient =

$$1-\left(\frac{\text{survival of a given ecotype in a given environment}}{\text{survival of that ecotype in the environment giving maximal survival}}\right)$$

At the seed, seedling, and adult stages, the environment giving maximal survival for *Dryas octopetala* ecotypes was from 2 to 25 times more favourable in terms of survival than the other environment. In addition, the more favourable environment at one stage was not necessarily so at another stage. In the fellfield ecotype, seed germination was favoured on the fellfield, yet seedling survival was higher in the snowbed (Table 5). The two ecotypes were remarkably similar in their responses to the environment at different stages in that in no case (where significant discrimination existed) was one site the better site for one ecotype, and the other site the better site for the other ecotype. This shows that selection has not been capable of perfectly matching the ecotype to the environment, but that the ecotypes have different relative advantages in environments that may be disadvantageous to both.

Reciprocal transplants have drawbacks due to the persistence of the effects of past development in a different environment (acclimatization, a within-generation effect), or of development of parents in a different environment (carry over, a between-generation effect). This problem is relevant to the separation of genetic and environmental

TABLE 5. Environmental discrimination coefficients (defined in text) for *Dryas octopetala* ecotypes reciprocally transplanted in home and foreign sites in Alaska. Significance levels are calculated from comparisons of means of values in Table 3 by *t*-test or (in the case of adults) by a test of equality of two percentages. Symbols: * $P < 0{\cdot}05$; ** $P < 0{\cdot}01$; *** $P < 0{\cdot}001$; $^{\mathrm{NS}}$ not significant. Significance levels refer to differences from a value of 0 (no environmental discrimination).

Ecotype	Site	Pollination success	Seed germination	Seedling survival			Adult survival
				Winter	Summer	1 year	
Fellfield	Fellfield	0	0	0·89**	0	0·85*	0
	Snowbed	$0{\cdot}55^{\mathrm{NS}}$	0·85**	0	$0{\cdot}25^{\mathrm{NS}}$	0	0
Snowbed	Fellfield	$0{\cdot}32^{\mathrm{NS}}$	0	0·89***	0·74***	0·97***	0·50**
	Snowbed	0	$0{\cdot}63^{\mathrm{NS}}$	0	0	0	0

components of the phenotype (Baskin & Baskin 1973; Quinn & Colosi 1977; Hume & Cavers 1981). On the other hand, where the purpose of a transplant experiment is to examine selection experimentally, it is sometimes important *not* to remove pre-conditioning effects. For example, fellfield pollen, before being transferred by a pollinator to the snowbed will be pre-conditioned on the fellfield under natural conditions. Likewise, seed development and parental development does occur on the fellfield prior to the dispersal of fellfield seed to the snowbed. In this manner, acclimatization and carry over effects may play important selective roles in natural and experimental situations. However, when the experiment is started with seedlings and adult plants, they may subsequently show residual effects of the growth environment prior to transplanting. To minimize such effects, the seedlings and adults were allowed to acclimatize (albeit for only 1 month) prior to the first census. We know of no published data which test the importance of pre-conditioning effects in reciprocal transplant experiments, but a comparison of seeds and ramets in a common-garden experiment revealed significant differences between the two source materials in one of two populations tested (Hume & Cavers 1981).

A second problem of reciprocal-transplant studies concerns the degree and type of selection which has already taken place within a sampled population. For example, the population of adult fellfield plants may have a different genetic composition from the seed population from which they were derived. A random sample of adult plants of the fellfield ecotype chosen for transplanting to the snowbed would therefore not be equivalent to the adults that would exist in the snowbed following selection from fellfield seed. However, adult fellfield plants (which had undergone selection in the fellfield) when transplanted to the snowbed would be expected to be less fit than those which had undergone selection in the snowbed. The present results show no selection through differential survival of adults in the snowbed. However, in the transplant of snowbed adults to the fellfield site, significant selection was observed, but it is impossible to know whether prior selection in the snowbed site biased the estimate of between-ecotype selection. Clearly, the pattern of within-population selection is potentially important in the interpretation of results of transplants of later life cycle stages. In the present study, since between-ecotype differences are large, selection within an ecotype probably did not obscure the interpretation of the reciprocal transplants.

Despite the drawbacks of reciprocal-transplant experiments, the technique is useful in demonstrating the operation of selective forces (Antonovics & Primack 1982). When extended to several life-cycle stages, it provides a means of revealing the important components of selection in a set of plants—long-lived perennials—which have previously been considered relatively intractable in evolutionary and ecological studies. Knowledge of the stages (life cycle) and modes (viability and fecundity) of selection is vital to understanding the mechanisms by which one genotype (or ecotype) has a greater fitness than another.

ACKNOWLEDGMENTS

We thank N. Christensen, B. Strain, D. Roach, J. Schmitt, and B. Moss for their helpful comments on the manuscript; A. Chester, K. McGraw, L. Stuart, P. Gluck, and N. Fetcher for help in the field; A. Chester for providing Fig. 1. This research was supported by National Science Foundation (U.S.A.) grants to the authors and to the Duke University Phytotron, and by a James B. Duke graduate fellowship (to J.B.M.).

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(*Received 17 January 1983*)