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EXPERIMENTAL ECOLOGY OF *DRYAS OCTOPETALA* ECOTYPES. III. ENVIRONMENTAL FACTORS AND PLANT GROWTH

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ABSTRACT

Environmental factors responsible for differential growth and fitness in fellfield and snowbed ecotypes of *Dryas octopetala* were examined. Field manipulations to alter levels of nutrient availability, water availability, exposure, and competition were performed in 1979, 1980, and 1981. Factors associated with nutrient availability and competition had the greatest effect on growth in both ecotypes. However, shading and fertilization treatments had strong negative effects on fellfield plants, whereas snowbed plants were more shade-tolerant and growth increased in response to fertilization.

Relative effects of nutrients and light were examined further in a factorial experiment under controlled conditions. The two ecotypes responded differently to variation in light level, reaffirming the ecotypic difference in shade-tolerance. However, unlike the results of field fertilization, high nutrient availability did not differentially affect the two ecotypes. Therefore, the differential response of ecotypes to high nutrient availability in the field was most likely due to an increase in the biomass and productivity of the competitors of *D. octopetala*. Field and growth chamber studies suggested that the snowbed ecotype was better able to withstand the diminished light availability associated with increased competition.

INTRODUCTION

Ecotypic differentiation in plant populations, by definition, is accompanied by niche differentiation (Turesson, 1922). Where the habitats preferred by contrasting ecotypes are adjoining, gene flow between populations is likely and the maintenance of genetic differences requires the continual removal of alien genes by natural selection (Jain and Bradshaw, 1966). In two cross-compatible ecotypes of *Dryas octopetala* L. (Rosaceae), genetic differences and separate spatial distributions are maintained by selection in this way (McGraw, 1982; McGraw and Antonovics, 1983a). Selection favors local plants over alien plants by differential survival and by differential growth and fertility. One ecotype (*Dryas octopetala* ssp.

octopetala) is a community dominant on exposed fellfield sites while the other ecotype (ssp. *alaskensis*) forms dense stands in areas of late-lying snow. Several environmental and vegetational factors differ between snowbed and fellfield sites and any of them could therefore be responsible for the pattern of selection observed. Given the fact that several factors change in concert along many types of environmental gradients, this pattern may be the rule rather than the exception. In Alaska, snowbed sites have higher nutrient and water availability, less exposure to wind and snowblast, and a shorter growing season than adjacent fellfield sites (Miller, 1982). The plant community at the snowbed site also has a greater total biomass, primary productivity, and plant cover than that at the fellfield site (Miller, 1982).

Past studies have attempted to determine the factors responsible for arctic or alpine species and community

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distributions by correlation analysis across many sites (Bliss, 1956; Scott and Billings, 1964; Klikoff, 1965; Miller, 1982). An alternative approach was used in the present study to determine what factors are responsible for the habitat-specificity of *Dryas octopetala* ecotypes. Field and growth-chamber manipulations of the factors which differed between snowbed and fellfield sites were performed, and the relative growth responses of the two ecotypes were observed. Miller (1982), working on a site 100 m from that used in the present study, suggested by correlation that nutrient availability was the major control over variation in community types along arctic snow-

bank gradients. I therefore hypothesized that the difference in nutrient availability between snowbed and fellfield sites could best explain the selection and distribution of *D. octopetala* ecotypes across the gradient. The effects of altering nutrient availability were compared with the effects of altering exposure, water availability, and level of interspecific competition in both sites. Factors most strongly affecting growth of *D. octopetala* under field conditions were varied under controlled conditions and growth responses were examined in greater detail with a growth chamber study.

FIELD STUDIES

STUDY SITE AND PLANT MATERIALS

The study site was located at an altitude of 1050 m in montane tundra near Eagle Summit, Alaska, at mile 106 on the Steese Highway (65°26'N, 145°30'W). The vegetation at the site was largely undisturbed tundra and had a strong floristic association with arctic tundra north of treeline. Snowbanks commonly form in the lee of mountain ridges near Eagle Summit and are important in determining the distribution of several tundra community types (Miller, 1982). Detailed descriptions of the study site and plant communities in the vicinity of such snowbanks may be found elsewhere (Miller, 1982; McGraw and Antonovics, 1983a).

Dryas octopetala is found in several of the tundra communities in the vicinity of snowbanks, but it is most abundant in two of these; the snowbed and the fellfield. Snowbed plants are found primarily in a 5- to 20-m wide band inside the snowbank edge (at the position of maximum extent). The plants have relatively large (15 to 50 mm) evergreen leaves and grow in a prostrate, clonal manner with adventitious rooting by the woody stems. Fellfield plants are found primarily on exposed ridgetops. They are easily distinguished from snowbed plants because they have small (5 to 15 mm) deciduous leaves and a dense mat-forming growth habit. Taxonomically designated subspecies (Hultén, 1959), the two populations have been experimentally shown to be genetically distinct (McGraw and Antonovics, 1983a). Due to their consistent association with specific habitats, they were designated ecotypes (*sensu* Turesson, 1922).

MANIPULATIONS

Four environmental "factors" were varied experimentally in the natural communities extant in fellfield and snowbed sites: levels of competition, drought stress, nutrient availability, and exposure. The experiments were designed to alter the physical environment primarily with respect to those factors. The factors were chosen because they have been shown in other studies to vary across environmental gradients created by snowbanks (Bliss, 1956; Rochow, 1970; Billings, 1973; Oberbauer and Miller, 1979; Miller, 1982) and all are known to be capable of affecting plant survival and reproduction.

Manipulations were carried out in fellfield and snow-

bed sites in a rectangular set of 1 × 1 m plots. Each plot was separated from neighboring plots by a 1-m-wide "buffer" strip. Five replicate plots were set up for each treatment in a completely randomized block design. All manipulations were carried out for three successive growing seasons, beginning in 1979.

Competitive effects were examined in two ways. In one manipulation, aboveground parts of all plant species except *Dryas octopetala* were removed from the plot. Removals were carried out three times in 1979 and twice in 1980, as required to trim back leaves and stems which resprouted from roots or rhizomes. In 1981, clipping was done only once early in the season. Competitors were then allowed to grow undisturbed in order to determine whether the removals had a significant long-term effect on the standing biomass of competing species. Tundra species are well known for their ability to resprout from roots or rhizomes (Billings and Mooney, 1968). If little resprouting occurred, the removal treatment probably affected competition above- and belowground. However, if resprouting resulted in normal levels of aboveground growth over an entire growing season, the effect of repeated clipping would have been primarily to remove shoot competition. In a second treatment, shade cloth tents were erected over plots to decrease light availability during the growing season, simulating increased "competition" for light. The shade cloth lowered light levels to approximately 25% of ambient photosynthetically active radiation.

Water availability was reduced in the snowbed site by erecting a 1 × 1 m clear plastic sheet 40 to 50 cm above plots at the snowbed site. This rain shield was sloped to allow rain to run off. To prevent surface runoff from wetting the plots, each plot was trenched 10 cm outside the plot edge. Measurements made on 13 July 1980 under clear, warm conditions indicated that the daily maximum soil surface temperatures were not increased by the plastic rain shields, although the minimum daily temperatures were up to 4°C higher. Light reduction by the shields was minimal. Water additions were made on fellfield plots with water taken from nearby inundated frostboils. Five liters per application were spread evenly with a watering can over each 1 × 1 m plot in an amount equivalent to a rain of 0.5 cm. This treatment was applied twice weekly

in 1979 and once weekly in 1980. The summer of 1981 was extremely wet at the field site (McGraw et al., 1983), and soils were continually saturated. Therefore water additions were discontinued.

Nutrient manipulations were performed in a manner similar to that of Shaver and Chapin (1980). Nitrogen was applied in the form of ammonium nitrate at a rate of $15 \text{ g m}^{-2} \text{ yr}^{-1}$ in three applications in the first year and at a rate of $10 \text{ g m}^{-2} \text{ yr}^{-1}$ in two applications per year in 1980 and 1981. The rate of application was lowered in the second and third years because some species exhibited necrosis (manifested by browning of leaves) in midseason at the higher level. In a similar manner, phosphorus was applied in the form of phosphate at the rate of $15 \text{ g m}^{-2} \text{ yr}^{-1}$ in 1979 and $10 \text{ g m}^{-2} \text{ yr}^{-1}$ in 1980 and 1981, in three and two applications, respectively. Starch was added at a rate of $25 \text{ g m}^{-2} \text{ yr}^{-1}$ at the same time nutrient applications were made in order to lower nutrient availability. Addition of readily available carbon substrates (such as starch) to soils has been previously shown to increase microbial population growth, concomitantly increasing microbial demand for soil nutrients (Turner, 1977). Starch or sugar additions have sometimes resulted in significantly reduced vascular plant growth when applied to tundra soils (Shaver, pers. comm., 1981), and this is thought to be the result of lower nutrient availability.

Two factors correlated with differential exposure in snowbed and fellfield sites were examined: exposure to wind and growing season length. The intensity of high winds on the fellfield was reduced to simulate reduced exposure in the snowbed by erecting a 20-cm-high barrier (constructed of thin transparent fiberglass sheets) in the shape of an "E" over each of five $1 \times 1 \text{ m}$ plots. The shape of the barrier was intended to slow wind speeds at 10 cm above the tundra surface to less than ca. 15 km h^{-1} at all times as was normally the case at the snowbed site. Measurements with a hand-held anemometer during winds gusting to more than 80 km h^{-1} indicated that the manipulation was largely successful, although occasional gusts or erratic wind direction changes resulted in momentary wind speeds higher than 15 km h^{-1} . One side of each plot was not barricaded (the open side of the "E") in order to prevent stagnation of air and subsequent temperature increases within plots. The barriers were erected in 1979, 1980, and 1981.

The growing season was lengthened in the snowbed by digging through 2 to 3 m of snow in May and exposing a $2 \times 2 \text{ m}$ plot. The excavation was performed at approximately the same time that fellfield plants were beginning to produce new leaves. While conditions in the exposed plot were not equivalent to concurrent conditions on the fellfield, the growing season of exposed plants was successfully lengthened relative to that of surrounding snowbed plants by 3 to 4 wk. In August 1979, a 3.5-m pole was erected on the southeast corner of the snow-removal plot in the snowbed site to aid in relocation of the plot in subsequent years. The snow removal treatment was carried out in May in all three years.

On the fellfield, the growing season was shortened to

simulate the growing season in the snowbed by adding snow cover for 3 to 4 wk until snowbed plots emerged from the receding snowbank. This snow addition plot was located near the other fellfield manipulations outside of the randomized block and it was maintained throughout the study.

The final set of plots in both sites were controls in which no manipulations were performed. Frequencies and levels of all treatments are summarized in Table 1.

RESPONSE MEASUREMENTS

Three sets of plant growth responses were measured in manipulation plots corresponding to first, second, and third year effects. In the first two years of the treatments, shoot responses were studied nondestructively. Twenty shoots of *D. octopetala* in each plot were tagged at random with numbered jewelry tags for a total of 100 shoots per treatment. In 1979, shoot size was estimated by counting the number of mature and immature leaves on each tagged shoot. In 1980, the same shoot populations were censused again. Shoot death, growth of tagged shoots and new shoot production was noted. These parameters were integrated into an overall measure of shoot population growth: 1980 shoot population size divided by the 1979 shoot population size. In *D. octopetala*, shoot population growth is an important component of fitness because of its role in determining the number of meristems which can be converted to flowers (McGraw and Antonovics, 1983b).

By 1981, many tags were lost or identification numbers were illegible due to weathering. Therefore, no shoot population measures could be made in the third year. Instead, 1981 shoot growth was determined with a destructive harvest on those treatments which previously showed the strongest shoot responses. The harvest was performed in August 1981 after shoot growth by most species had ceased. Aboveground 1981 shoot growth was clipped from all vascular plant species in two $20 \times 20 \text{ cm}$ quadrats per plot. The two quadrats were located on pre-specified coordinates on a diagonal within each $1 \times 1 \text{ m}$ plot. Collected samples were separated by species in each quadrat and subsequently dried in field drying ovens at 65°C . They were redried before final weight determinations were made. In the data analysis of harvested plots, graminoids (primarily grasses and sedges) were lumped into one category since their identity was uncertain without flowers available for keying purposes. In addition, since there were 32 species harvested in the plots, all other species (primarily dicotyledonous) were categorized as either forbs or shrubs to simplify data presentation and to discern general trends among growth forms.

RESULTS OF FIELD STUDIES

Factors Related to Competition

At the fellfield site, removal of competing species resulted in a slight increase in mean shoot size for *D. octopetala* in 1979 (*t*-test only, Table 2). In 1980, fellfield plants in removal plots showed a significantly higher

TABLE 1
Field manipulations carried out at Eagle Summit, Alaska

Treatment	Site		Frequency	Level
	Fellfield	Snowbed		
Control	x	x		
Competitive factors				
Removal	x	<i>x</i> ^a	1979:3; 1980:2; 1981:1	Complete weeding
Shading	<i>x</i>	x	1979-1980: continuous in growing season	75% light reduction
Water availability				
Water addition	x	—	1979: 2/wk; 1980: 1/wk 1981: —	0.5 cm
Water reduction	—	x	1979-1981: continuous	See text
Nutrients				
N addition	x	x	1979:3; 1980-1981: 2	5 g m ⁻²
P addition	x	x	(same)	5 g m ⁻²
NP addition	x	x	(same)	5 g m ⁻²
Starch	x	x	(same)	25 g m ⁻²
Exposure				
Wind barrier	x	—	1979-1981: continuous	See text
Snow addition	x	—	1979-1981: each spring	See text
Snow removal	—	x	1979-1981: each spring	See text

^aAn italicized *x* indicates a treatment in which the factor manipulation was intended to shift that factor in the direction of its value at the foreign site.

TABLE 2
Mean leaf number per shoot in field factor manipulations

Treatment	Fellfield Ecotype				Snowbed Ecotype			
	Mean (S.E.)	% of control	<i>T</i> ^a	<i>MRT</i>	Mean (S.E.)	% of control	<i>T</i>	<i>MRT</i>
Control	4.39 (.11)				6.60 (.24)			
Removal	4.70 (.11)	107	*	ns	6.79 (.24)	103	ns	ns
Shading	4.08 (.11)	93	*	ns	5.16 (-2.0)	78	*	*
Water addition	4.26 (.11)	97	ns	ns	—	—	—	—
Water reduction	—	—	—	—	6.74 (.21)	102	ns	ns
N addition	5.18 (.16)	118	*	*	6.92 (.24)	105	ns	ns
P addition	4.74 (.13)	108	*	ns	4.96 (.22)	75	*	*
NP addition	5.47 (.16)	125	*	*	7.23 (.21)	110	*	ns
Starch addition	4.30 (.10)	98	ns	ns	6.89 (.19)	104	ns	ns
Wind barrier	4.66 (.13)	106	ns	ns	—	—	—	—
Snow addition	5.05 (.11)	115	*	*	—	—	—	—
Snow removal	—	—	—	—	6.60 (.18)	100	ns	ns

^aMeans for factor manipulations are compared with controls with a *t*-test (*T*) and with the more conservative Duncan's multiple range test (*MRT*). ns, not significantly different from controls; *, significantly different with *p* < 0.05.

TABLE 3
Shoot population growth rates^a in field manipulations

Treatment	Fellfield Ecotype				Snowbed Ecotype			
	Mean (S.E.)	% of control	<i>T</i> ^b	<i>MRT</i>	Mean (S.E.)	% of control	<i>T</i>	<i>MRT</i>
Control	1.21 (.05)				1.29 (.05)			
Removal	1.47 (.08)	121	*	*	1.51 (.11)	117	ns	ns
Shading	0.86 (.05)	71	*	*	1.35 (.14)	105	ns	ns
Water addition	1.06 (.05)	88	ns	ns	—	—	—	—
Water reduction	—	—	—	—	1.50 (.18)	116	ns	ns
N addition	0.99 (.04)	82	*	ns	1.95 (.25)	151	*	*
P addition	1.16 (.11)	96	ns	ns	1.37 (.13)	106	ns	ns
NP addition	1.34 (.13)	111	ns	ns	1.49 (.14)	116	ns	ns
Starch addition	1.10 (.07)	91	ns	ns	1.55 (.07)	120	*	ns
Wind barrier	1.09 (.05)	90	ns	ns	—	—	—	—
Snow addition	1.21 (.07)	100	ns	ns	—	—	—	—
Snow removal	—	—	—	—	1.25 (.10)	97	ns	ns

^aShoot population growth rate was calculated as the 1980 shoot population size divided by the 1979 shoot population size.

^bStatistical comparisons as in Table 2.

TABLE 4
Aboveground production (g m⁻²) in 1981 in field manipulations

Treatment	Community component	Fellfield Site			Snowbed Site		
		Mean	(S.E.)	<i>F</i> ^a	Mean	(S.E.)	<i>F</i>
Control	Shrubs	5.73	(1.65)		17.53	(5.73)	
	Forbs	2.20	(1.53)		17.30	(4.75)	
	Graminoids	3.60	(1.88)		18.33	(2.83)	
	<i>D. octopetala</i>	65.53	(10.40)		21.70	(4.43)	
	Total	77.03	(8.88)		74.86	(8.70)	
Removal	Shrubs	0.50	(0.40)	5.06*	7.23	(4.25)	1.85
	Forbs	3.88	(2.00)	0.46	11.20	(4.18)	0.96
	Graminoids	3.58	(2.03)	0.00	15.10	(6.03)	0.83
	<i>D. octopetala</i>	47.03	(13.00)	0.94	33.25	(11.93)	1.80
	Total	54.98	(11.48)	1.78	66.78	(3.75)	0.33
Shading	Shrubs	10.38	(3.35)	1.16	1.50	(0.75)	5.88*
	Forbs	4.30	(1.80)	0.41	15.25	(3.55)	0.11
	Graminoids	6.88	(1.73)	0.92	19.60	(3.08)	0.00
	<i>D. octopetala</i>	17.83	(8.33)	6.42*	24.00	(6.93)	0.01
	Total	39.38	(7.93)	5.06*	60.33	(7.03)	0.22
Starch addition	Shrubs	2.65	(0.83)	1.94	4.40	(1.50)	4.07
	Forbs	2.30	(1.03)	0.00	12.10	(2.43)	0.65
	Graminoids	3.05	(1.00)	0.05	22.90	(4.95)	0.32
	<i>D. octopetala</i>	44.73	(12.10)	1.27	27.93	(5.53)	0.62
	Total	52.75	(12.13)	1.94	67.33	(7.98)	0.27

^a*F*-statistics are provided for one-way analysis of variance comparing treatments with controls for each community component. *, significant at $p < 0.05$.

shoot population growth rate than those in control plots (Table 3). However, aboveground production in 1981 was not different from controls (Table 4). At the snowbed site, removal of competitors had no effect in any of the three years.

The shading treatment reduced the mean leaf number per shoot at the fellfield site (*t*-test only, Table 2) and shoot population growth declined as well (Table 3). In 1981, aboveground production was significantly lower for *D. octopetala* in shaded plots than in control plots. Since *D. octopetala* accounted for 85% of total aboveground production in controls, total community production was significantly reduced as well. In the snowbed, the effects of shading were less pronounced. Shading reduced shoot size (Table 2), but had no effect on shoot population growth or aboveground production in snowbed *D. octopetala*.

After three growing seasons of reduced light availability, the contrasting response of fellfield and snowbed *Dryas octopetala* was especially conspicuous in the context of the community response. At the fellfield site, shading reduced aboveground production by *Dryas octopetala* from 85% of the total to 45%. Although aboveground production by snowbed *D. octopetala* did not change significantly in absolute amount with shading, there was a slight increase in percent of total production (from 29% in controls to 40% with shading).

Water Availability

The tundra vegetation at Eagle Summit, Alaska, is found on permafrost soils. The seasonal melting of the permafrost keeps at least part of the soil profile wet throughout the growing season. A previous study showed that drought stress is uncommon in the regional vegetation (Oberbauer and Miller, 1979). The present study was consistent with the previous work in that attempts to alter the water status of the soil with water addition (fellfield) or water reduction (in the snowbed) had no effect in 1979 or 1980. Aboveground production in 1981 was therefore not determined for these treatments.

Nutrient Availability

Addition of nutrients had strong effects on *Dryas octopetala*. These effects changed with time at the fellfield site. Addition of nitrogen (N), phosphorus (P), and nitrogen + phosphorus (NP) caused an increase in shoot size in 1979 (Table 2). Leaf necrosis associated with excess nitrogen was evident with N addition in 1980, and shoot population growth was significantly less than that of controls (*t*-test, Table 3). NP addition had no effect on shoot population growth. In 1981, fertilization with N reduced aboveground production by *D. octopetala* in the fellfield (Figure 1). In contrast, production by graminoids increased. In the analysis of variance, the net effect of N addition on total aboveground production was positive (Table 5, Figure 1). Addition of P also decreased aboveground production by *D. octopetala*, but the combined effects of N and P showed a positive interaction between the two nutrients (Table 5). As a result of this interac-

tion and a trend toward a positive interaction in graminoids, the NP interaction was significant for total aboveground production as well (Table 5).

At the snowbed site, fertilization had strong effects,

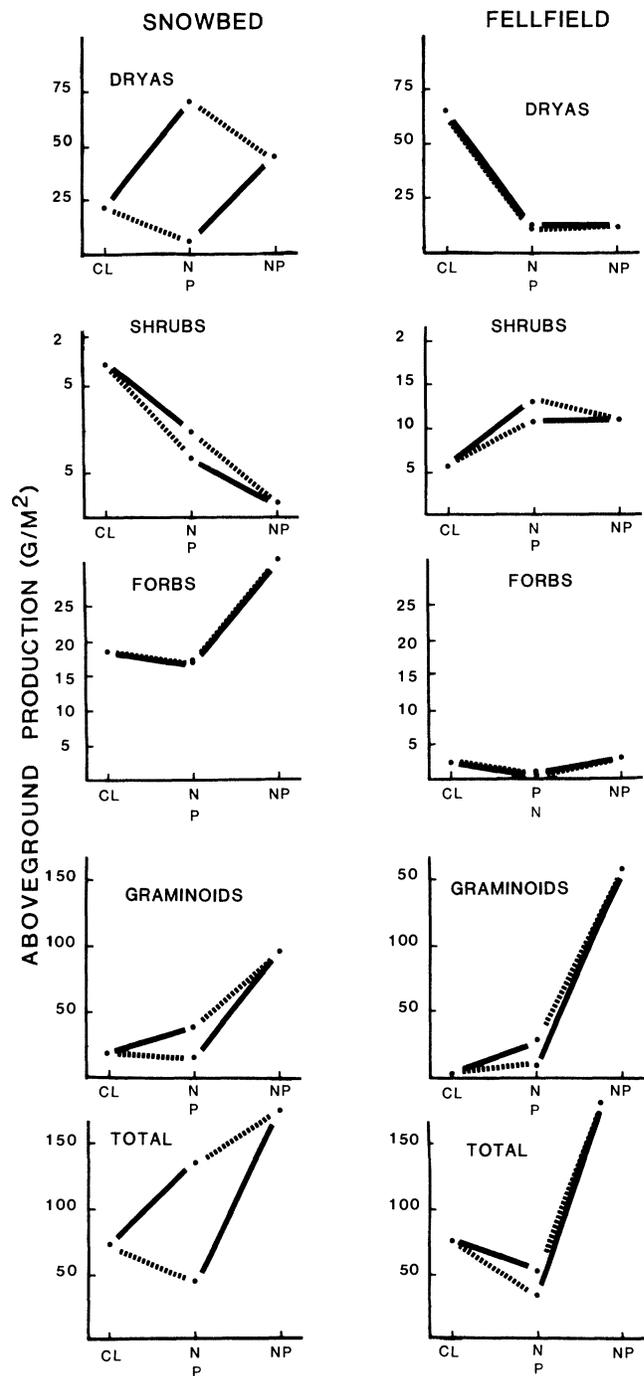


FIGURE 1. Response of aboveground production by various growth forms and *Dryas octopetala* to fertilization with nitrogen (N), phosphorus (P), and nitrogen plus phosphorus (NP) as compared to control plots (CL) in which no fertilizer was added. Solid lines indicate the effect of nitrogen and dotted lines indicate the effect of phosphorus. *n* = 10 for each point.

TABLE 5
Significance levels for fertilizer treatments
in field experiments

Community component	Source of Variation ^a					
	Fellfield Site			Snowbed Site		
	N	P	NP	N	P	NP
Shrubs	ns	ns	ns	ns	*	ns
Forbs	ns	ns	ns	ns	ns	ns
Graminoids	**	ns	ns	***	*	*
<i>D. octopetala</i>	**	**	**	***	*	ns
Total (all components)	*	ns	*	***	ns	*

^aTwo-way analysis of variance for 1981 aboveground production; ns, not significant; *, $p < 0.05$; **, $p < 0.01$; ***, $p < 0.001$.

as in the fellfield. Addition of NP resulted in larger shoots in 1979 (Table 2). Addition of P decreased shoot size in terms of live leaf number by causing leaf necrosis and leaf death. In 1980, shoot population growth was greater with N addition than in controls and the shoot population size nearly doubled in 1 yr (Table 3). Aboveground production was also most strongly affected by addition of N. In contrast to the response of fellfield plants, fertilization with N increased production by both graminoids and *Dryas octopetala* (Table 5). The net effect of N addition on total aboveground production was positive (Figure 1, Table 5). Phosphorus addition had a positive effect on aboveground production of graminoids, but a negative effect on *Dryas octopetala* (Figure 1) and other shrubs. A positive interaction between N and P effects was seen in graminoids and therefore an interaction was also seen in total aboveground production (Table 5).

The contrast in the responses of fellfield and snowbed

ecotypes of *D. octopetala* is emphasized in the context of the community response to fertilization. Total aboveground production in both communities increased by an identical factor of 2.4 with NP addition. In the fellfield community, production by graminoids increased from 5% of the total aboveground production to 86% with NP addition. The trend in relative aboveground production of *D. octopetala* was almost exactly the reverse; a decrease from 85% of the total (controls) to 6% with NP addition. In the snowbed, relative aboveground production by graminoids increased from 24% to 54% of the total. At the same time, production by *D. octopetala* remained about the same (29% in controls, 24% with NP addition). The increase in production by graminoids in the snowbed was primarily at the expense of shrubs (23% of total aboveground production in controls, <1% with NP addition), and not *D. octopetala*.

The attempt to lower nutrient availability with starch addition had little effect. In the fellfield, there were no significant differences between controls and starch addition plots in shoot size, shoot population growth, or aboveground production. In the snowbed, starch addition significantly increased shoot population growth over that of controls. However, this trend was statistically significant only with the *t*-test and not with the more conservative multiple range test (Table 3). No other growth parameter was significantly altered by starch addition.

Exposure

Wind barriers and snow addition increased shoot size slightly in 1979 at the fellfield site but had no effect on shoot population growth. Aboveground production was therefore not measured.

Snow removal from the snowbed site had no effect on either shoot size or shoot population growth. Aboveground production was not measured.

CONTROLLED ENVIRONMENT STUDIES

METHODS

In field manipulations, alterations of light and nutrient availability in fellfield and snowbed sites had the largest effect on growth of *Dryas octopetala*. In addition, snowbed and fellfield plants responded differently to these factor manipulations. Therefore, effects of light and nutrient availability were examined in detail under controlled conditions.

Seeds were collected from *Dryas octopetala* plants at the field site in August 1979 and taken to Duke University where they were placed in a freezer at -17°C . Full seeds of fellfield and snowbed plants were selected using a dissecting microscope. On 4 February 1980, these seeds were placed on moist filter paper in petri dishes in growth chambers at 17°C ($150 \mu\text{mol m}^{-2} \text{s}^{-1}$, continuous light). On average, seeds of the fellfield ecotype germinated 1 to 3 d prior to seeds of the snowbed ecotype. On 11 and 12 February, seeds with emerged radicles were placed in separate pots containing "Turface." Seedlings were kept

well watered and continued to emerge and grow for 5 d under germination conditions. Seventy-five seedlings of each ecotype were then moved to each of four conditions in growth chambers at the Duke University Phytotron. Light and nutrient levels were varied in a 2×2 factorial manner. The two nutrient levels were (1) half-strength Hoagland's solution applied twice weekly (high nutrients) or (2) half-strength Hoagland's solution applied once every 2 wk (low nutrients). The photosynthetic photon flux densities were $500 \mu\text{mol m}^{-2} \text{s}^{-1}$ in the high light treatment and $20 \mu\text{mol m}^{-2} \text{s}^{-1}$ in the low light treatment. Other factors were held constant in the course of the experiment. Relative humidity was set at 75%. The photoperiod was 15 h for the first 6 wk of the experiment and 14 h for the last 2 wk. Temperatures were maintained at 17°C in the light and 4°C in the dark. Seedlings were harvested 54 to 56 d after being placed in the growth chambers. Number of active meristems, number of leaves, and length of the longest leaf were determined for each seed-

ling. Groups of five seedlings were lumped for determinations of mean root and aboveground weights. Roots and aboveground parts were dried at 70°C for at least 24 h and weighed. The data were subjected to three-way analysis of variance with light, nutrients, and ecotype as main effects. Results of the factorial experiment were depicted separately for each ecotype with a graphical technique adapted from Richards (1941).

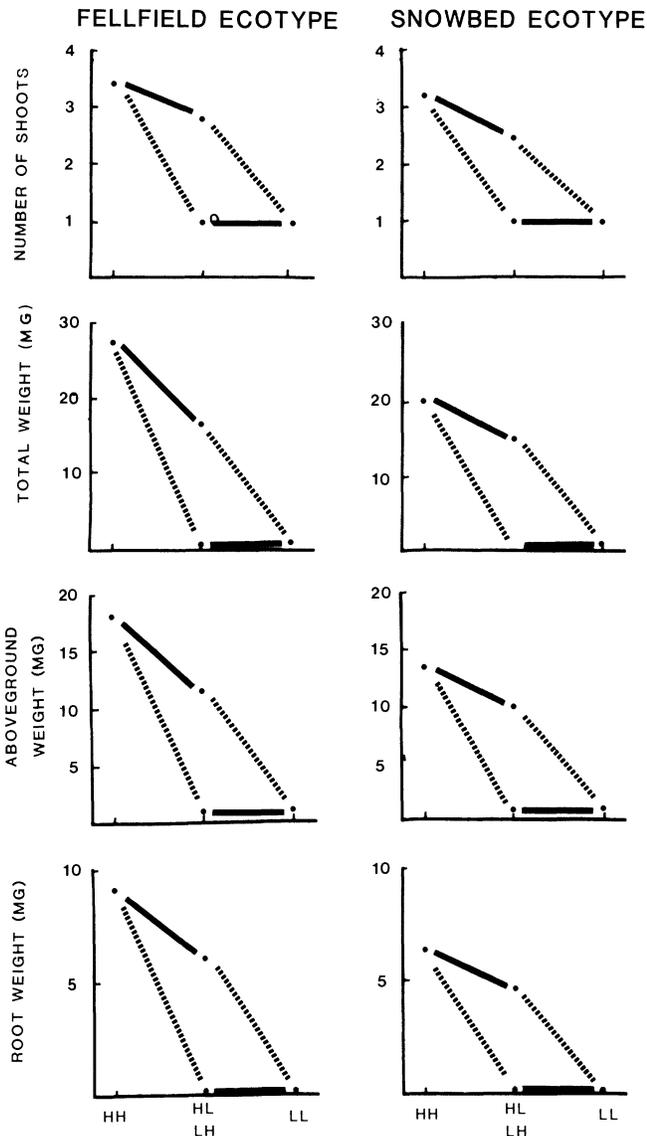


FIGURE 2. Effect of light and nutrients on measures of plant performance for the fellfield ecotype and the snowbed ecotype grown in controlled growth chamber conditions. Solid lines indicate the effect of reducing nutrient availability and dotted lines indicate the effect of reducing light level. HH, high light, high nutrients; HL, high light, low nutrients; LH, low light, high nutrients; LL, low light, low nutrients. $n=75$ for each treatment.

RESULTS

Light level had strong effects on seedling growth and morphology. Shading reduced all performance indices of plant growth including shoot number and root, aboveground, and total weight in both ecotypes (Figure 2, Table 6). In addition, low light levels reduced leaf length and the root:shoot ratio (Figure 3, Table 6). Low nutrient availability also reduced plant growth (Figure 2), although its effects on leaf size and allocation to roots vis-à-vis shoots were not significant (Figure 3, Table 6). The fellfield ecotype had greater root production than the snowbed ecotype (Table 6) and a trend was observed toward greater total biomass production ($p < 0.09$). The fellfield ecotype also had a higher root:shoot ratio than the snowbed ecotype (Table 6). Snowbed plants had significantly longer leaves than the fellfield plants (Table 6), as expected since leaf size is one of the major features distinguishing the two ecotypes.

The effect of high levels of either nutrients or light was more pronounced in the presence of high levels of both factors (a positive light/nutrient interaction; Table 6). The only other significant interaction in plant growth measures was an ecotype/light interaction; root weight in the fellfield ecotype was more sharply reduced by shading than root weight in the snowbed ecotype. As a result, a light/ecotype interaction was also revealed by the analysis for root:shoot ratio. Total weight and leaf length tended to decrease more with shading in the fellfield ecotype than in the snowbed ecotype ($p < 0.06$ and $p < 0.10$, respectively). There were no statistically significant differences in the way that the two ecotypes responded to

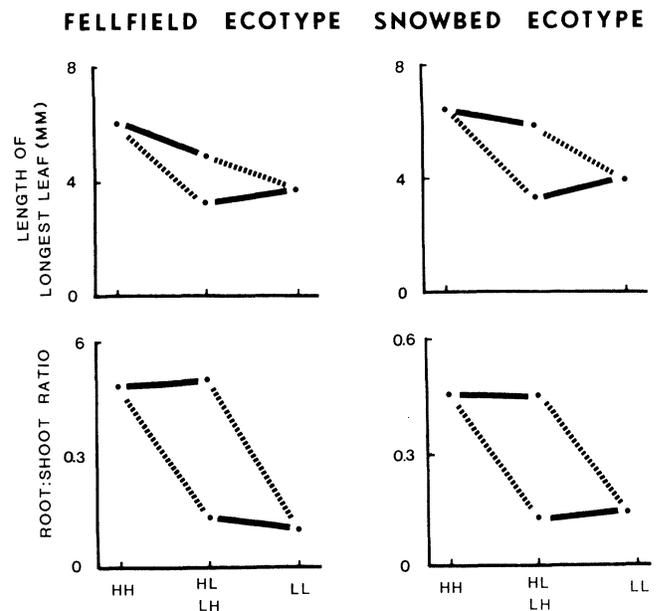


FIGURE 3. Effect of light and nutrients on leaf size and allocation to roots and shoots for the fellfield ecotype and the snowbed ecotype in controlled growth chamber conditions. Notation as in Figure 2. $n=75$ for each treatment.

TABLE 6
Effects of ecotype (E), light (L), nutrients and factor interactions on growth

Growth measure	Source of Variation ^a						
	E	L	N	ExL	ExN	LxN	ExLxN
Root weight	*	***	*	*	ns	*	ns
Aboveground weight	ns	***	*	ns	ns	**	ns
Total weight	a	***	*	a	ns	ns	ns
Number of shoots	ns	***	***	ns	ns	***	ns
Length of longest leaf	**	***	ns	a	a	***	ns
Root:shoot	**	***	a	***	ns	ns	ns

^aThree-way analysis of variance. ns, not significant; *, $p < 0.05$; **, $p < 0.01$; ***, $p < 0.001$; a, approaches significance ($0.05 < p < 0.10$).

variation in nutrient level (i.e., no nutrient \times ecotype interaction). However, a trend was observed toward a greater reduction of leaf length under low nutrient conditions in

the fellfield ecotype than in the snowbed ecotype ($p < 0.07$). There was no significant three-way interaction in any of the measured parameters.

DISCUSSION

Ridgetop environments in mountains of interior Alaska have been reported to be drier, more exposed in winter, lower in nutrient availability, and lower in vascular plant cover than snowbed environments (Miller, 1982). These relative characteristics are common in other alpine areas as well (Billings and Mooney, 1968; Bliss, 1971). A differential response to any of these factors could result in natural selection among ecotypes of a species found in both environments. Ecotypes, if locally adapted, should respond to an experimental shift in a selectively important factor in a predictable way. For example, if the level of the factor is shifted toward that found in a foreign site, the shift should be detrimental to plant growth and fitness.

Several of the manipulations reported in the present study were attempts to shift the level of a particular factor toward that found at the foreign site (treatments with italicized \times in Table 1). These manipulations showed that fellfield *Dryas octopetala* was relatively unresponsive to a reduction in exposure to wind (wind barriers), to a shortened growing season (snow addition), or to an augmented water supply (water addition). Although these factors cannot be disregarded as selective agents against the fellfield ecotype in the snowbed environment, the magnitude of their effects is too low to explain the observed strength of selection (McGraw, 1982; McGraw and Antonovics, 1983a). Much more effective in reducing performance of fellfield plants were manipulations of light and nutrients. The shading response was not unexpected. However, the relative responses of the two ecotypes to the same light reduction regime suggested that the snowbed ecotype was better able to adjust to low light than was the fellfield ecotype. This would, in turn, suggest that the snowbed ecotype could better tolerate shading by taller competitors.

Addition of nutrients to the fellfield site produced an unexpected result. Not only was the growth response of fellfield *Dryas octopetala* less than that of the snowbed ecotype, but by the third year aboveground production had actually declined with fertilization. With addition of both nitrogen and phosphorus (NP addition), this effect was not due to leaf necrosis. Rather, it was probably due to increased competition. The reversal in dominance (percent of total aboveground production) of graminoids and *Dryas octopetala* suggested that the increase in production by graminoids may have occurred at the expense of production by *D. octopetala*. The proliferation of graminoids was accompanied by greater tiller densities and greater canopy height, resulting in shading of the more prostrate *D. octopetala*. The resemblance between the response of fellfield plants to shading and the response to NP addition was striking. In shaded plots, aboveground production by *D. octopetala* declined to 17.8 g m^{-2} , while in NP plots, aboveground production decreased to 11.5 g m^{-2} (from 65.5 g m^{-2} in controls). These data provide correlative evidence that enhanced interspecific shoot competition stimulated by greater nutrient availability may eliminate fellfield plants from the snowbed environment.

In the field, the effect of a differential tolerance to shading by other plants would be enhanced by the genetic difference in leaf morphology of the ecotypes. The snowbed ecotype has a greater potential for producing large leaves than the fellfield ecotype (McGraw and Antonovics, 1983a). These larger leaves are held erect and therefore can reach higher into the canopy than the small, erect leaves of the fellfield plants. They therefore intercept more light in competition with shoots of surrounding plants. As a result, not only are snowbed plants better able to tolerate severe shading, they are also less likely

to encounter such conditions due to their growth form. The ability to produce large leaves should be particularly advantageous during seedling establishment when virtually all competitors would be taller than the seedling. Selective advantage in a strain of subterranean clover (*Trifolium subterraneum*) was attributed to longer petioles and leaves in a similar manner by Black (1960).

Factors responsible for selection against the snowbed ecotype in the fellfield environment were not clearly revealed by the manipulations. Removal of competing species, reduction of water availability, starch addition (an attempt to lower nutrient availability), and lengthening of the growing season did not significantly depress growth of snowbed plants. Although nutrient additions and shading affected growth of snowbed plants, these treatments did not shift factor levels toward those on the fellfield; their primary importance was to compare the relative responses of fellfield and snowbed ecotypes. For practical reasons, no attempt was made to simulate the effect of winter snowblast and desiccation. However, those factors, to which snowbed plants are not normally exposed, are potentially powerful selective agents (Warren Wilson, 1959), especially since snowbed plants retain their leaves for two full growing seasons. Adult and seedling snowbed plants transplanted to the fellfield (McGraw and Antonovics, 1983a) were exposed to all of the factor differences between sites and did not retain live leaves until spring. Presumably leaf death occurred either by desiccation or physical abrasion caused by windblown snow. This loss of leaf area would be expected to reduce potential carbon gain by the plant since leaves in their second season normally remain photosynthetically active (McGraw, 1982).

Field factor manipulations are often unavoidably crude. The frequency and level of a manipulation cannot readily mimic that of a factor in another environment. Moreover, it is not possible to dismiss the possibility of factor interactions in the field. Most of the manipulations performed in the present study probably altered factors other than those intended, at least to some degree. This aspect of field manipulations is not necessarily the nuisance that it appears to be, for if an artificial change in an environmental factor affects other factors, natural changes (e.g., along a natural gradient) may do so as well. However, it does confound the interpretation of the cause

of a plant response; in this case, the selection among ecotypes. Therefore, complementary studies are required to separate factor effects under controlled conditions.

The growth chamber studies substantiated the hypothesis derived from field manipulations concerning the cause of selection against fellfield plants in the snowbed. The fellfield ecotype was negatively affected by reduced light availability, more so than the snowbed ecotype. The fellfield ecotype responded positively to increased nutrient availability in the controlled environment, unlike in the field. However, this apparent contradiction suggests that increased competition due to fertilization was the cause of decreased growth of fellfield *Dryas octopetala* in the field, and not greater nutrient availability per se.

Recent studies of species distributions have emphasized the potential importance of interactions among factors (see Connell, 1983, for a review). The present study demonstrates the probable role of factor interactions in the distribution of genetically distinct populations within a species and in the action of natural selection between these populations. The original hypothesis that nutrient availability was the principal determinant of the distribution and selection of ecotypes must now be modified. Enhanced nutrient availability in the snowbed environment probably results in a greater standing biomass and productivity of competing species (shrubs, forbs, and graminoids). This enhanced vegetative cover, in turn, reduces light availability. The field and growth chamber studies strongly suggest that it is this combination of conditions that favors the snowbed ecotype in a snowbed environment. The advantage may be attributed to a greater physiological tolerance for shade in the snowbed ecotype as well as the morphological plasticity in leaf size which allows the snowbed plants to produce large leaves at the snowbed site.

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