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SIZE, STRUCTURE, AND HABITAT CHARACTERISTICS OF POPULATIONS
OF *BRAYA HUMILIS* VAR. *HUMILIS* (BRASSICACEAE):
AN ALPINE DISJUNCT FROM COLORADO

Elizabeth E. Neely¹ and Alan T. Carpenter²

ABSTRACT.—Size, structure, and habitat characteristics were studied in three populations of *Braya humilis* var. *humilis* (C. A. Meyer) Robins. in Gray & Wats. (Brassicaceae), a small, herbaceous perennial of the alpine tundra in central Colorado. There was a significant association between numbers of reproductive, juvenile, and seedling individuals and population location. Plant size within reproductive, juvenile, and seedling size classes varied significantly among three populations. Plots containing *Braya* had significantly lower total plant cover, a different set of dominant plant species, more rock, bare ground, and less litter than plots without *Braya*. *Braya* appears to be restricted to calcareous substrates that experience a moderate level of disturbance, such as solifluction lobes and abandoned roads. Populations are small despite the existence of much potential habitat. Population studies are necessary for active conservation management of *Braya*.

Braya humilis var. *humilis* (C. A. Meyer) Robins. in Gray & Wats. (Brassicaceae) is a small, herbaceous perennial that occurs in the alpine tundra of the Rocky Mountains in central Colorado. It is a rare taxon, disjunct from its nearest relatives in Canada by approximately 1,600 km. The isolated populations in Colorado were previously treated by Rollins (1953) as *B. humilis* ssp. *ventosa*. However, recent monographic work by Harris (1985), based on greenhouse and common garden studies, indicates that the Colorado plants should be treated with *B. humilis* var. *humilis*. In North America *Braya humilis* var. *humilis* occurs from Alaska, south through the northern Rocky Mountains to Alberta and British Columbia, north through the western Canadian Arctic Archipelago, east to Greenland, Newfoundland, Anticosti Island, Vermont, and the north shore of Lake Superior (Harris 1985). Colorado populations of *B. humilis* may represent isolated relicts left behind on small areas of calcareous alpine habitat as glaciers retreated about 12,000 years before present (Harris 1985). Hereinafter, *Braya* will refer to *Braya humilis* var. *humilis*.

In Colorado, *Braya* is restricted to calcareous soils derived from Paleozoic rock formations such as the Mississippian Leadville Limestone and Ordovician Manitou Dolomite (Tweto 1974). The plant commonly grows in

association with *Dryas octopetala*, *Carex rupestris*, and *Kobresia myosuroides* on exposed slopes without late-lying snowbanks. It is often found growing in solifluction lobes, on low-angle scree slopes, and on gravel with minor amounts of soil movement, but it also grows on man-made disturbances such as old mining roads and prospects.

In Colorado, *Braya* is known to exist only in 19 small isolated populations at 12 general locations in the Mosquito, Ten Mile, Elk, and Collegiate ranges. At nearly all of its known occurrences in Colorado, *Braya* populations are small despite the existence of much apparent potential habitat. Approximately 3,900 individuals exist in Colorado, based on estimates for each known population. It is a taxon of special concern in Colorado (O'Kane 1986) and is currently a candidate for listing (Category 2) by the U.S. Fish and Wildlife Service under the Endangered Species Act (Fay 1985).

Counts of one population west of Hoosier Pass, Colorado, have varied greatly, suggesting considerable year-to-year fluctuation in numbers (Harmon 1980, Johnston 1984, Neely 1985). Unfortunately, the accuracy of these counts is questionable because the plants are small and easily overlooked. Accurate counts are important for determining the size and dynamics of populations and are fun-

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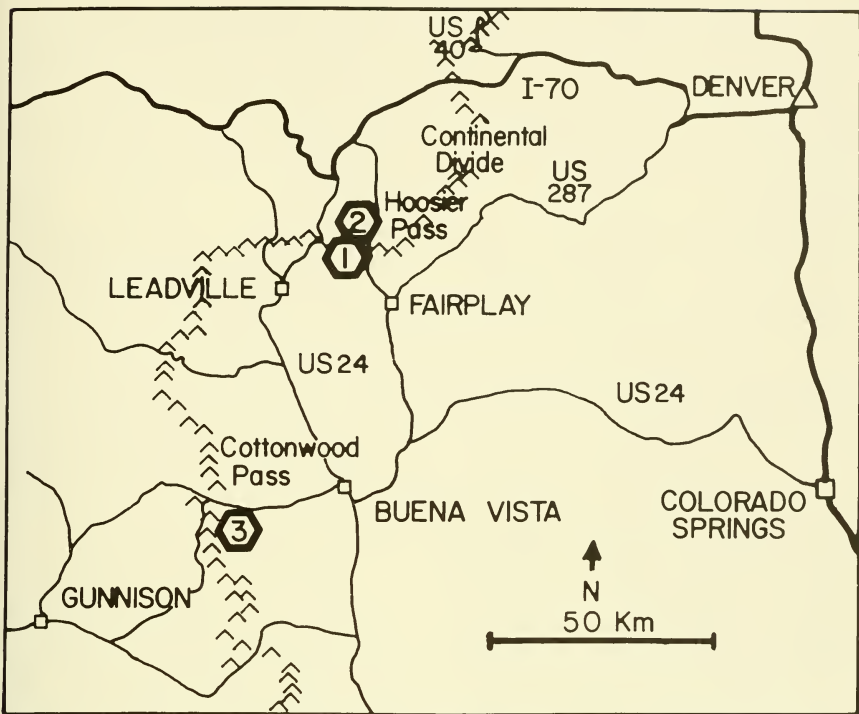


Fig. 1. Locations of the three study sites in central Colorado. 1 = Mt. Bross, 2 = West Hoosier, and 3 = Spout Lake.

damental to the conservation management of the taxon (Bradshaw and Doody 1978).

Relatively few population studies have been undertaken on long-lived perennials, particularly those that are rare. There is increasing recognition by plant conservationists of the need to monitor rare plant populations to determine population structure, flux, and modes of population regulation (Bradshaw and Doody 1978, Whitson and Massey 1981, Kruckeberg and Rabinowitz, unpublished manuscript).

We initiated in 1985 a long-term study of *Braya* population dynamics, selecting three populations in locations that span a gradient from minimal to substantial human disturbance. First-year objectives were to determine if significant variation among and within populations existed for (a) numbers of plants in three size classes and (b) size characteristics of plants. Additional objectives were to deter-

mine if vegetation and substrate characteristics at one of the locations differed between (c) microsites containing *Braya* and those that did not, and (d) microsites containing *Braya* on and off an old vehicle track.

METHODS

Three populations were chosen for study (Fig. 1, Table 1). Both the Mt. Bross and West Hoosier sites have experienced great historical mining activity and are dissected by old roads and prospects. Mt. Bross is particularly important because it has the largest known population, with an estimated 1,160 individuals (Johnston 1984). The West Hoosier site is significant because it has the second largest population (approximately 430 individuals). Part of the West Hoosier site is owned and managed as a preserve by The Nature Conservancy. The Spout Lake population, the only

TABLE 1. General location descriptions for three *Braya humilis* var. *humilis* populations in central Colorado.

Descriptor	Location		
	Mt. Bross	West Hoosier	Spout Lake
County	Park	Park/Summit	Chaffee
Latitude/longitude	39°19'N, 106°06'E	39°22'N, 106°05'E	38°47'N, 106°25'E
Mountain range	Mosquito	Ten Mile	Collegiate
Elevation (m)	3758	3695	3750
Aspect	East-southeast	East-southeast	North
Slope (degrees)	0-30	20-30	30-40
Human disturbance	High	High-low	Low
Dominant vascular plant species	<i>Poa rupicola</i> , <i>Draba aurea</i> , <i>Arenaria obtusiloba</i>	<i>Dryas octopetala</i> , <i>Carex rupestris</i> , <i>Kobresia myosuroides</i>	<i>Dryas octopetala</i> , <i>Carex rupestris</i> , <i>Kobresia myosuroides</i>

record from the Collegiate Range, consists of approximately 210 individuals and has the largest known population on a site with no evident human disturbance.

Monitoring

Thirty-two permanent, 1-m² plots were established at the three locations in August 1985 (22 plots at Hoosier, 4 plots at Mt. Bross, and 6 plots at Spout Lake). Alternate corners of the plots were marked with iron spikes 25 cm long. An iron nail was driven into the ground adjacent to each *Braya* plant; an aluminum tag was attached to each nail. Plant coordinates within the plots were recorded on data forms to facilitate relocation of individual plants in future years. Measurements of rosette diameter and height and counts of numbers of stems, leaves, flowers and fruits were recorded for all *Braya* individuals within the plots. Sampling methodology was adapted from that used by D. W. Inouye and M. B. Cruzan (personal communication) in central Colorado and was conducted during 10 to 15 August 1985.

Plants were separated into three size classes based on their development; ages could not be determined. Seedlings were defined as nonreproductive plants with five or fewer leaves. Juveniles were plants with more than five leaves but without current year's flowers or fruits. Reproductive individuals had current year's flowers or fruits present.

G-tests were used to test for significant association between numbers of *Braya* plants in the three size classes and location. Plant size data were tested for normality using an algorithm in Minitab (Ryan et al. 1982) and were normalized using logarithmic transfor-

mation where appropriate. Data were subjected to analysis of variance (ANOVA) to determine if plant size characteristics differed significantly among locations. T-tests were used to assess statistical significance of differences in plant size characteristics on and off the old vehicle tract (termed the cutoff road) within the West Hoosier population.

Vegetation and Substrate Sampling

Total cover of vascular plant species, cover by species, and cover of substrate components (rock, bare ground, and litter) were estimated to the nearest percent for 22 permanent 1-m² plots containing *Braya* and 22 randomly placed 1-m² plots that did not contain *Braya* at the West Hoosier location. Similar data were collected for plots containing *Braya* on and off the cutoff road. Data were tested for normality as outlined above, transformed as needed, and analyzed using ANOVA. T-tests were used to assess significance of differences in total vegetal cover, cover of dominant vascular plant species, and substrate cover between plots (a) containing or not containing *Braya* and (b) on or off the cutoff road.

RESULTS

Size Structure of Populations

Size structure of *Braya* populations differed among the three locations with a highly significant association between the number of plants in each size class and location (Table 2). Mt. Bross had the largest proportion of seedlings, whereas West Hoosier had the lowest. West Hoosier had the highest proportion of reproductive individuals. Spout Lake had the same proportion of juveniles as did West

TABLE 2. Number (and percentage) of *Braya* plants in three size classes at three locations in central Colorado. Reproductive class includes individuals with current year's flowers or fruits. Juvenile and seedling classes include individuals possessing no current year's reproductive material and that have >5 leaves or 1-5 leaves per plant, respectively.

Plant size class	Location		
	Mt. Bross	West Hoosier	Spout Lake
Reproductive	95 (29%)	139 (47%)	24 (18%)
Juvenile	72 (22%)	139 (47%)	63 (47%)
Seedling	164 (49%)	19 (6%)	47 (35%)
Total	331	297	134

There is a highly significant association ($P < 0.005$) between plant class and location (G-test, Sokal and Rohlf 1981).

TABLE 3. Measures of *Braya* plant size and reproductive output in three size classes at three locations in central Colorado. Means \pm 1 SEM. For definitions of plant classes, see Table 2. Different letters in parentheses within each row denote significantly different means ($P < .05$, least significant difference test, Zar 1974).

Plant size class	Location			
	Mt. Bross	West Hoosier	Spout Lake	P-value
REPRODUCTIVE				
Height (mm)	34.8 \pm 1.5(a)	30.2 \pm 1.2(b)	20.7 \pm 1.6(c)	<0.001
# of stems/plant	4.4 \pm 0.5(a)	2.7 \pm 0.2(b)	1.4 \pm 0.5(c)	<0.001
# of fruits/plant	22.9 \pm 0.2(a)	12.1 \pm 1.4(b)	6.7 \pm 1.2(c)	<0.001
# of leaves/plant	28.1 \pm 1.4(a)	23.6 \pm 1.0(b)	16.8 \pm 1.5(c)	<0.001
Rosette diameter (mm)	27.4 \pm 1.0(a)	21.4 \pm 0.8(b)	20.4 \pm 1.1(b)	<0.001
JUVENILE				
# of leaves/plant	9.9 \pm 0.7(a)	12.7 \pm 0.6(b)	13.1 \pm 0.8(b)	<0.001
Rosette diameter (mm)	12.8 \pm 0.7(a)	10.8 \pm 0.4(b)	13.4 \pm 0.6(a)	<0.006
SEEDLING				
# of leaves/plant	4.1 \pm 0.1(a)	4.9 \pm 0.1(b)	3.5 \pm 0.1 (c)	<0.001
Rosette diameter (mm)	5.5 \pm 0.2	5.9 \pm 0.6	6.2 \pm 0.4	0.178

Hoosier, but it had a much higher proportion of seedlings.

The height, number of stems, fruits, and leaves per plant and rosette diameter of reproductive individuals were significantly different among the three locations (Table 3). Reproductive plants at Mt. Bross were consistently the largest and produced the most reproductive material. Spout Lake consistently had the smallest reproductive individuals; they also produced the smallest amount of reproductive material.

The number of leaves per plant and rosette diameter of juvenile individuals were significantly different among the three locations (Table 3). The Spout Lake juvenile plants were the largest. There were significant differences in the number of leaves per seedling among sites, but not in rosette diameter.

The proportions of plants in the three size classes were significantly different on and off the cutoff road at West Hoosier (Table 4). The plants on the road were mostly reproductive, whereas the plants off the road were mostly

juveniles. Although the proportion of seedlings on the road was twice that off the road, seedlings were scarce in both areas. The number of leaves per plant and the diameter of reproductive individuals, as well as the rosette diameter of juveniles, were significantly greater on the road (Table 5).

Vegetal and Substrate Cover

Total vascular plant cover and cover of *Dryas octopetala*, *Carex rupestris*, and *Kobresia myosuroides* were significantly lower on the cutoff road at West Hoosier (Table 6). Plots on the road had significantly greater cover of rock but significantly less litter cover than plots off the road. There was little evidence of disturbance off the road.

Plots containing *Braya* had significantly less total vascular plant cover and cover of *Dryas octopetala*, *Kobresia myosuroides*, and *Polygonum viviparum* than plots lacking *Braya* (Table 7). The rank order of the three plant species with the greatest cover was different in *Braya* plots compared to plots lack-

TABLE 4. Number (and percentage) of *Braya* plants in three size classes on and off the cutoff road at the West Hoosier location in central Colorado. For definitions of plant classes, see Table 2.

Plant size class	Location	
	On cutoff road	Off cutoff road
Reproductive	61 (59%)	78 (40%)
Juvenile	39 (37%)	100 (52%)
Seedling	4 (4%)	15 (8%)
Total	104	193

There is a highly significant association ($P < 0.005$) between plant class and location (G-test, Sokal and Rohlf 1981).

ing the plant. The substrate of *Braya* plots was characterized by significantly greater rock and bare ground but lower litter cover.

DISCUSSION

Size Structure and Populations

The different proportions of reproductive, juvenile, and seedling individuals that were observed at the three locations could arise from differences in recruitment, survival, or growth of *Braya* plants. Recruitment of seedlings in harsh environments such as the alpine is probably episodic for many plant species (Billings 1974, Jolls 1982). Factors affecting recruitment could vary substantially over distances on the order of several kilometers. Thus, *Braya* seedling recruitment at the three sites could vary widely among and within years. The small size and large numbers of seedlings at Mt. Cross may indicate more recent establishment at this location, with the few seedlings at West Hoosier resulting from lack of recent recruitment.

Survival of plants within all size classes could also vary greatly among locations and years. The combined effects of differential recruitment and survival could perhaps account for the large observed differences in proportions of size classes at the three locations.

The variation in plant size structure among populations could arise from differential plant growth rates, caused by site quality differences such as soil fertility, soil moisture, length of the growing season, or competition from other species. Difference in rosette diameter may be a phenotypic response to these varying site conditions.

Very little is known about recruitment, survival, and growth of *Braya* individuals. Thus, it is unknown how rapidly the present class

structure could change, implications of which are important for the conservation of the taxon. For example, the West Hoosier population consists of reproductive and juvenile individuals with very few seedlings. This population might be senescent with poor prospects for long-term survival. Alternatively, the present dearth of seedlings could simply reflect several recent years of poor seedling establishment, with former seedlings moving into the juvenile and reproductive classes. We presently lack the information necessary to make rational management prescriptions for *Braya*.

Subpopulations only a few meters apart also had different size structures. The lower proportions of juvenile and seedling individuals on the cutoff road may have resulted from increased mortality in the smaller size classes caused by soil erosion on the road. Reproductive individuals, which were nearly always larger than juveniles or seedlings, may have survived better because of their more extensive root systems.

Harris (1985) has reported that *Braya* is octoploid ($2n = 56$). Polyploidy may be an important factor in *Braya*'s success on old roads. Polyploids are more likely to become adapted to environments disturbed by human activity than are their related diploids (Clegg and Brown 1983). Polyploidy helps to buffer against inbreeding depression and may enhance wide environmental tolerance. Autogamy and polyploidy may help maintain the extremely isolated populations in Colorado (Harris 1985).

Substrate and Plant Associates

Braya microsites at West Hoosier are rocky with much bare ground, minimal litter, and sparse vegetal cover. Typical substrate consists of about 50% rock fragments 1–3 cm in length and about 50% bare ground. Our observations of substrates at other *Braya* locations were consistent with these findings. The low total vegetal cover on the cutoff road is consistent with the findings of Greller (1974), who found total plant cover on 40- to 50-year-old roadcut slopes in the alpine tundra of Rocky Mountain National Park to be less than half of the surrounding natural sites.

Past and Present Disturbance

Braya appears to be a pioneer species of

TABLE 5. Measures of *Braya* plant size and reproductive output in plots on and off the cutoff road at West Hoosier. Means \pm 1SEM. For definitions of plant classes, see Table 2.

Plant size class	Location		P-value
	On cutoff road	Off cutoff road	
REPRODUCTIVE			
Height (mm)	30.3 \pm 1.9	30.2 \pm 1.5	0.96
Number of stems/plant	3.0 \pm 0.4	2.4 \pm 0.3	0.17
Number of fruits/plant	13.9 \pm 2.3	10.7 \pm 1.6	0.24
Number of leaves/plant	26.9 \pm 1.7	21.1 \pm 1.0	0.003
Rosette diameter (mm)	24.2 \pm 1.3	18.8 \pm 0.7	0.000
JUVENILE			
Number of leaves/plant	13.6 \pm 1.3	12.3 \pm 0.7	0.35
Rosette diameter (mm)	13.2 \pm 0.9	10.0 \pm 0.5	0.001
SEEDLING			
Number of leaves/plant	4.8 \pm 0.2	5.0 \pm 1.7	0.49
Rosette diameter (mm)	7.2 \pm 0.2	5.5 \pm 0.7	0.23

TABLE 6. Cover of dominant (>1% cover) vascular plant species and substrate components in *Braya* plots on and off the cutoff road and plots off the cutoff road not containing *Braya* at West Hoosier. Means (%) \pm 1 SEM.

	Location			P-value
	<i>Braya</i> plots on road	<i>Braya</i> plots off road	Plots without <i>Braya</i>	
PLANT SPECIES				
<i>Dryas octopetala</i>	0.1 \pm 0.0	12.3 \pm 3.9	30.5 \pm 5.7	0.001
<i>Carex rupestris</i>	0.8 \pm 0.3	6.5 \pm 2.3	2.8 \pm 1.0	0.060
<i>Kobresia myosuroides</i>	0.9 \pm 0.4	5.8 \pm 2.3	10.8 \pm 2.5	0.030
<i>Erigeron pinnatisectus</i>	2.0 \pm 0.6	1.8 \pm 0.6	2.8 \pm 0.8	0.056
<i>Polygonum viviparum</i>	1.3 \pm 0.3	2.2 \pm 0.5	4.5 \pm 0.8	0.556
<i>Hymenoxys acaulis</i>	absent	2.2 \pm 0.6	1.7 \pm 0.6	—
<i>Calamagrostis purpurascens</i>	1.0 \pm 0.6	1.8 \pm 0.5	2.4 \pm 0.8	0.483
<i>Silene acaulis</i>	absent	1.8 \pm 1.5	1.3 \pm 0.9	—
Total vascular plants	9.8 \pm 1.2	39.8 \pm 5.3	70.7 \pm 5.7	0.000
SUBSTRATE COMPONENTS				
Rock	58.1 \pm 5.5	25.1 \pm 5.3	16.4 \pm 3.2	0.000
Bare ground	35.0 \pm 4.9	46.5 \pm 4.9	22.5 \pm 4.2	0.002
Litter	2.0 \pm 0.5	7.5 \pm 1.2	17.4 \pm 2.2	0.000

TABLE 7. Cover of dominant (>1% cover) vascular plant species and substrate components in plots with and without *Braya* at West Hoosier. Means (%) \pm 1 SEM.

	Location		P-value
	Plots with <i>Braya</i>	Plots without <i>Braya</i>	
PLANT SPECIES			
<i>Dryas octopetala</i>	7.3 \pm 2.6	30.5 \pm 5.7	0.001
<i>Carex rupestris</i>	4.2 \pm 1.4	2.8 \pm 1.0	0.45
<i>Kobresia myosuroides</i>	3.8 \pm 1.5	10.8 \pm 2.5	0.02
<i>Erigeron pinnatisectus</i>	1.9 \pm 0.4	2.8 \pm 0.8	0.29
<i>Polygonum viviparum</i>	1.8 \pm 0.4	4.5 \pm 0.8	0.005
<i>Hymenoxys acaulis</i>	1.3 \pm 0.4	1.7 \pm 0.6	0.58
<i>Calamagrostis purpurascens</i>	1.4 \pm 0.5	2.4 \pm 0.8	0.29
<i>Silene acaulis</i>	1.0 \pm 0.9	1.3 \pm 0.9	0.86
Total vascular plants	27.5 \pm 4.5	70.7 \pm 5.7	0.000
SUBSTRATE COMPONENTS			
Rock	37.6 \pm 5.2	16.4 \pm 3.2	0.0015
Bare ground	42.1 \pm 3.7	22.5 \pm 4.2	0.0011
Litter	5.4 \pm 1.0	17.4 \pm 2.2	0.0000

disturbed areas. In some populations, only a few individuals have been found off these disturbances (E. E. Neely, personal observation). Congeners grow on unstable substrates, such as scree slopes, gravel bars, shorelines, and solifluction lobes (Harris 1985). Many rare taxa in the western flora of North America and their common relatives colonize disturbed habitats (Stebbins 1980). *Braya* may inhabit unstable or disturbed areas because of an inability to compete with other species, as suggested by Griggs (1940) for other species of rare plants.

Of the three populations, Mt. Cross plants appear to be the most vigorous, perhaps because past disturbance has reduced the density or size of other plants, leaving more resources available to *Braya*. The largest plants and those with the greatest amount of reproductive output at Mt. Cross occur mostly on the margins of a rough vehicle path and on spoil banks adjacent to a ditch. The path is level, and the surface is apparently stable. At West Hoosier, the cutoff road is considerably more disturbed than the adjacent areas. Possibly the degree of disturbance on the road is greater than optimum for *Braya*, given the virtual absence of seedlings and small proportion of juveniles.

Observations of *Braya* in the Spout Lake population reinforce the importance of soil disturbance. Here it typically grows in small gravels, scree slopes, and solifluction lobes that have been demonstrated in Rocky Mountain National Park, Colorado, to move downhill at a rate of 3–4 cm year⁻¹ (Benedict 1970). *Braya* appears to be preadapted to unstable substrates, making it most successful where there has been some moderate level of natural or man-made disturbance.

The sizes of *Braya* populations before human intervention began is unknown, but if populations at relatively undisturbed sites such as Spout Lake are any indication, populations must have been small. In some cases human disturbance may simulate natural processes that create suitable habitat; however, drastic disturbances such as mine-related activities could greatly reduce or eliminate populations. Because *Braya* is found on calcareous soils derived from rocks such as limestone, which are often highly mineralized, it may be threatened by potential mining activities.

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