OBSERVATIONS ON ALPINE VEGETATION NEAR SCHOOLROOM GLACIER, TETON RANGE, WYOMING

John R. Spence[1] and Richard J. Shaw[1]

Abstract.— Quadrat and propagule trapping studies were made on the moraine of the Schoolroom Glacier and in adjacent dry alpine meadow vegetation in the Teton Range in 1978–1979. Forty-six species of vascular plants were collected. Distributionally, three groups of species exist. One of these is concentrated primarily on the moraine, a second in the meadow, and the third in a narrow ecotonal band at the base of the distal slope of the moraine. The moraine slopes are steep and unstable, with vegetation cover ranging from 1 to 9 percent, dominated by *Cirsium tweedyi* (Rydb.) Petr. Along the more stable moraine crest the vegetation cover is heavier, and is similar to that in the meadow. The meadow vegetation cover is about 50 percent, dominated by *Astragalus kentrophyta* Gray. Using a combination of cover and frequency as a measure of importance, dominance-diversity curves were constructed for the moraine and meadow. Both approach geometric series, which are suggested as indicating harsh environments. Abiotically pollinated species are more successful on the moraine than biotically pollinated species, but the reverse is true for the meadow. Propagule trapping studies suggest that dispersal of anemochorous propagules onto the moraine is very low compared with dispersal in the meadow.

Relatively little is known about the structure and dynamics of alpine vegetation in the Teton Range, Grand Teton National Park, Wyoming. In this paper we report some preliminary quadrat and propagule trapping studies from alpine vegetation in the southern fork of Cascade Canyon in the center of the range.

The selected study area is a complex of alpine meadow and morainal deposits at the head of the south fork of Cascade Canyon, about 4 km southwest of the Grand Teton (Fig. 1). An east-facing cliff called The Wall bounds the study area on the west; this formation forms part of the hydrographic divide of the Teton Range. A shallow cirque has been carved into this cliff by the Schoolroom Glacier, so called because of the almost perfect end moraine fronting it (Fig. 2). The age of this moraine is unknown, but similar deposits elsewhere in the range are of Neoglacial age, which places the moraine age from about 100 to 3,000 years (Mahaney 1975, Mahaney and Spence 1983). Between this moraine and the glacier lies a small meltwater lake about 50 m across, which is drained by a stream that has cut through the center of the moraine. The two ends of the moraine merge into extensive talus derived from The Wall to either side of the glacier. Northeast of the glacier is a large outcrop of gneiss and schist of Precambrian age, which is vegetated by a mosaic of fen and timberline krummholz stands. To the east and southeast lies an extensive, slightly undulating dry alpine meadow underlaid by glacial and talus deposits of Pinedale or older age. The Wall and Schoolroom Glacier moraine are composed primarily of Death Canyon Limestone of the Gros Ventre Formation (Cambrian), with some debris of the Wolsey Shale member of the Gros Ventre Formation, in addition to Flathead Sandstone (Cambrian, Love, and Reed 1968, Reed 1973).

Climate data from the Teton Range and park are summarized elsewhere (Spence 1981). Mean annual temperature from Jackson Hole to the east of the range, at an elevation of 2,040 m, is about 1.3 C. Using the elevation of the study area, 3,060 m, and the adiabatic lapse rate (Cole 1975), average annual temperature in front of the Schoolroom Glacier would be about −4.8 C. Snow depth during the winter is unknown, but it is usually gone from the area by late June to early July during an average year. Common animals at the site include marmots (*Marmota flaviventris*), pikas (*Ochotona princeps*), and Rosy Finches (*Leucosticte atrata*).

The purposes of this paper are (1) to characterize and contrast the vegetation on the

[1]Department of Botany, University of British Columbia, Vancouver, B.C., Canada V6T 1W5.
[2]Department of Biology, Utah State University, UMC45, Logan, Utah 84322.

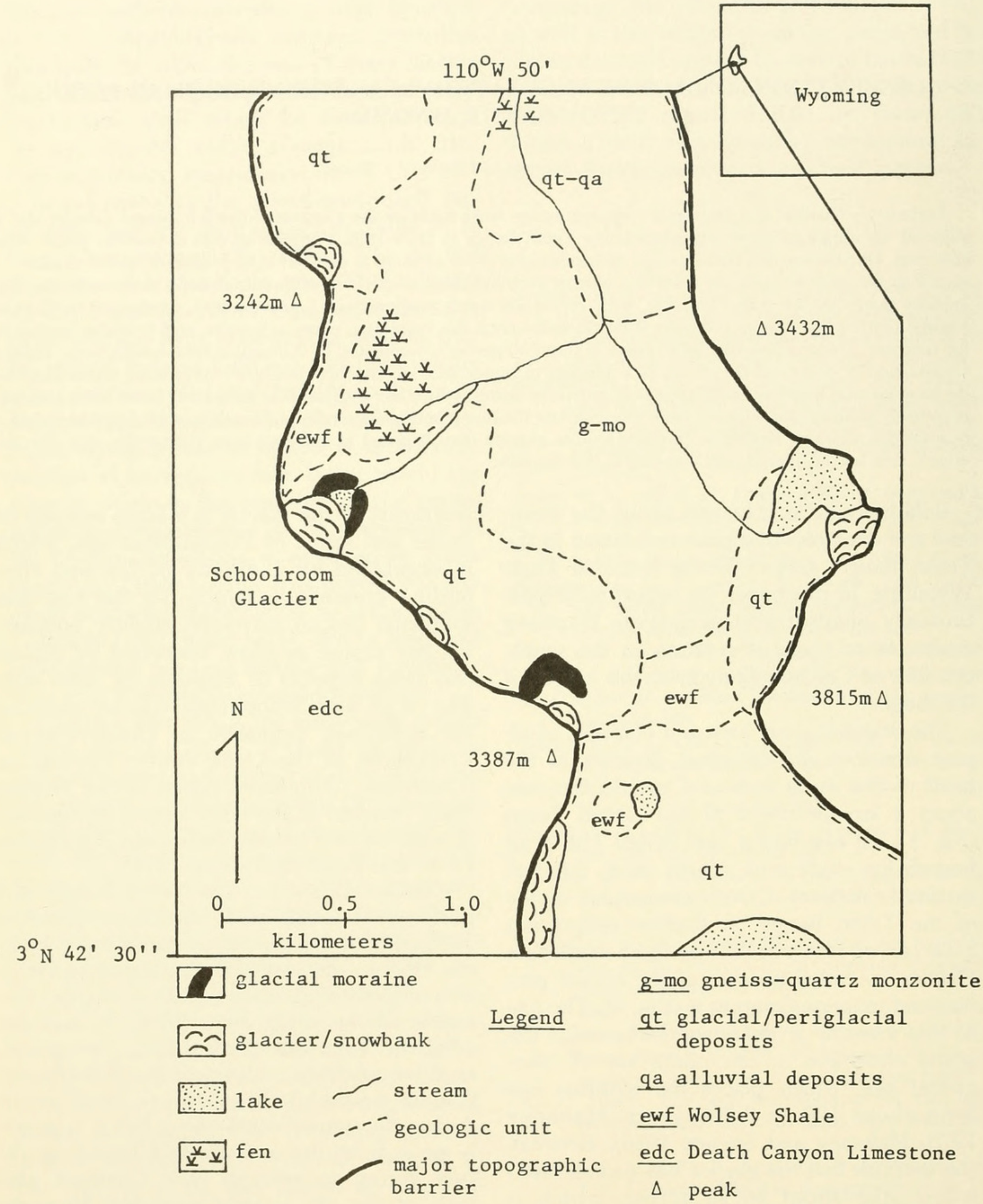

Fig. 1. A sketch map of the study area at the head of the south fork of Cascade Canyon. Only major features are shown on the map. The boundaries for the geologic units are only approximate. The map is derived from 7.5 minute USGS topographic maps, Love and Reed (1968), Reed (1973), and personal observations of the senior author (JRS). See the legend for map details.

Schoolroom Glacier moraine and in the dry alpine meadow adjacent to it, and (2) to suggest possible dynamics between the two communities.

Methods and Materials

Initial site observations and collections were made in the summer of 1978. In 1979,

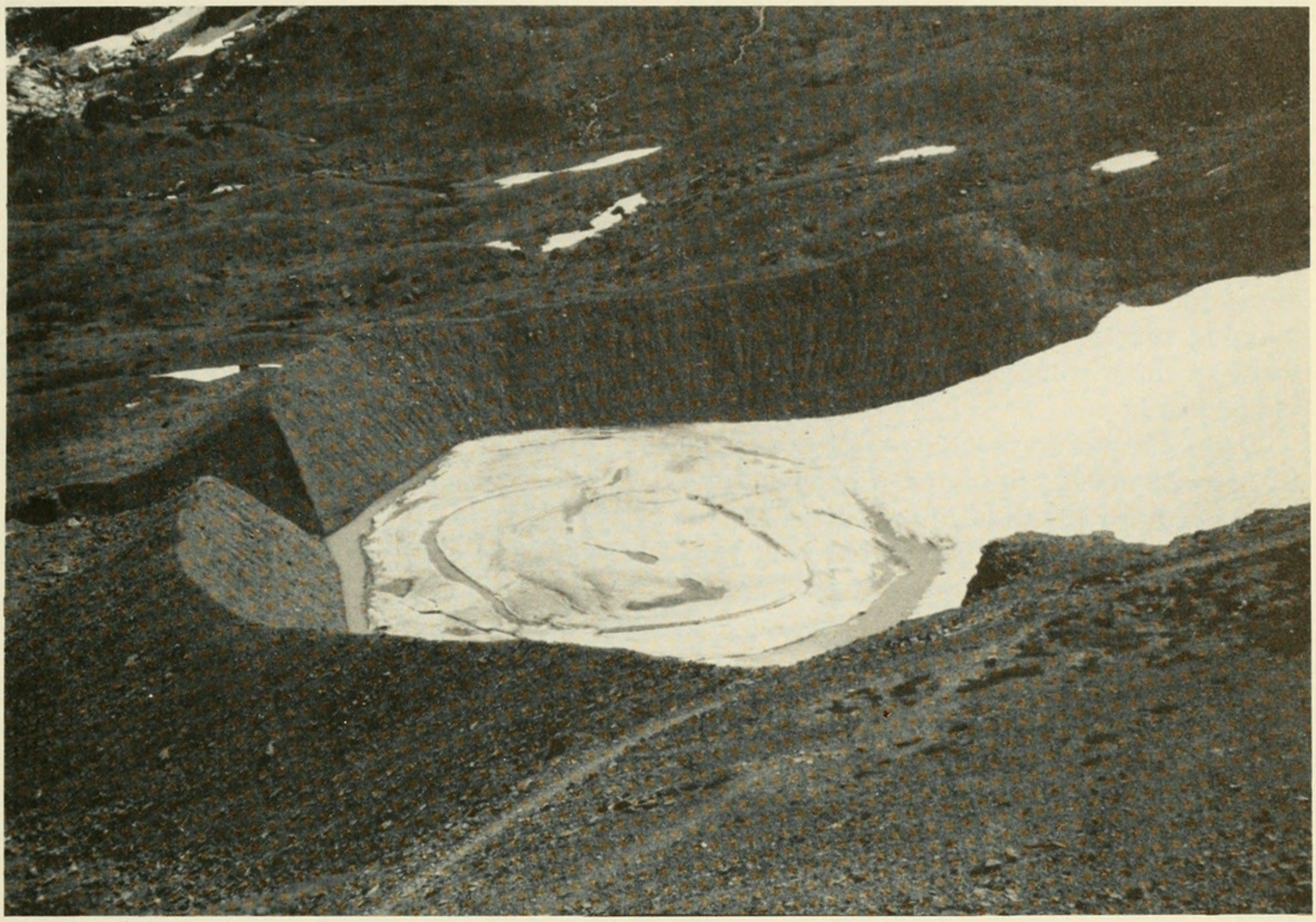

Fig. 2. Schoolroom Glacier at the head of the south fork of Cascade Canyon, Grand Teton National Park, Wyoming.

the quadrat data were gathered on 19 September. Two transects, each 90 m long, were run from the base of the proximal slope of the moraine adjacent to the meltwater lake, up to and over the moraine crest, down the distal slope, and out into the meadow. At 3 m intervals, a 0.5 × 0.5 m quadrat was placed down on alternating sides of the transect line. Cover and presence of all species was noted visually, using a modified Braun-Blanquet scale, as follows: + = 0–1 percent, 1 = 1–5 percent, 2 = 5–25 percent, 3 = 25–50 percent, 4 = 50–75 percent, 5 = 75–100 percent. For calculating the total and average cover values, the midpoints of the ranges were used. Prominence Values (PV) were calculated using the formula PV = percent cover × the square root of percent frequency. Along the transect lines, slope was measured using an Abney level.

Propagule trapping was studied in two ways, by water-filled plastic trays 40 × 15 × 5 cm in size, and 15 × 15 cm wooden plates coated with petroleum jelly. The water trays were used in 1978, with six of them placed in a line from the edge of the meltwater lake up and over the moraine to the meadow. In 1979, nine wooden plates were used, and were placed in a line 10 m apart from the edge of the lake up and over the moraine and out into the meadow. Once in July and once in September the wooden plates were in operation, for a total of 38 hours in July and 24 hours in September. This amounts to a total of 558 trap-hours in operation. Trapped propagules were placed in glass vials for later identification. A reference set of propagules from species at the site was made to aid in identification. Specimens collected are on deposit at the Moose Herbarium in Grand Teton National Park and the Intermountain Herbarium at Utah State University (UTC). Nomenclature follows Shaw (1976).

Results and Discussion

Forty-six species of vascular plants were collected from the moraine and adjacent meadow in 1978 and 1979. Details on the floristics and comparisons with other glacial moraine sites in the Tetons will be published elsewhere (Spence 1983). One species, *Taraxacum lyratum* Ledeb., is a new report for the park. The distribution of life forms of the species is: 1 shrub, 1 fern ally, 1 annual dicot, 11 graminoids, and 32 biennial/perennial forbs. Of these species, 31 were encountered along the two transects (Table 1). The remaining species are quite rare at the site, many of them consisting of only a few individual plants.

Along the first transect, average cover was 0.6 percent for the moraine proximal slope, 8.9 percent for the distal slope, and 47.4 percent for the meadow. For the second transect, the respective values were 2.8 percent, 9.2 percent, and 63.3 percent. Cover values per quadrat ranged from 0 percent (7 times; 6 on the moraine proximal slope, 1 on the moraine distal slope, and 0 in the meadow) to 106.5 percent (once, in the meadow). Pooling the results of the two transects, total cover on the moraine is 1.7 percent for the proximal slope and 9.1 percent for the distal slope. Average cover for the meadow is 54.6 percent. These values are all significantly different from one another at $\alpha = 0.05$. Data from the two transects are summarized in Table 1 for the moraine and the meadow.

Although most of the species encountered in the transects are found on both the moraine and in the meadow, they tend to be much more common on one or the other (see Table 1). General observations elsewhere on the moraine and in the meadow tend to sup-

TABLE 1. The quadrat data from the two line transects in summarized form. Each transect was 90 m long, with a 0.5 × 0.5 m quadrat placed at every 3 m interval, for a total of 60 quadrats and 15 m^2. The species are arranged alphabetically, and three numbers are listed for each species; percent frequency, average percent cover, and prominence value, which is calculated as average percent cover × square root of percent frequency. For details on transect placement and method of measuring species, see Methods and Materials.

Species	Moraine (N = 38)	Meadow (N = 22)
	(percent frequency/average percent cover/prominence value)	
Achillea millefolium	–	4.5/0.68/1.44
Agropyron caninum	10.5/0.54/1.75	22.7/4.25/20.25
A. scribneri	2.6/0.07/0.11	–
Antennaria umbrinella	7.9/0.09/0.25	45.5/4.82/32.51
Arabis lyallii	–	13.6/0.07/0.26
Arenaria nuttallii	–	13.6/0.07/0.26
Arnica longifolia	2.6/0.01/0.02	–
Astragalus kentrophyta	2.6/0.45/0.73	68.2/28.20/232.88
Carex species	–	9.1/0.14/0.42
Cirsium tweedyi	26.3/0.92/4.72	–
Cymopterus hendersonii	7.9/0.04/0.11	4.5/0.68/1.44
Epilobium alpinum	18.4/0.63/2.70	4.5/0.02/0.04
Erigeron compositus	7.9/0.14/0.39	13.6/0.34/1.25
E. leiomerus	–	4.5/0.68/1.44
Erysimum asperum	–	18.2/0.09/0.38
Festuca ovina	–	4.5/0.02/0.04
Hymenoxys grandiflora	2.6/0.01/0.02	72.7/4.20/35.81
Oxyria digyna	2.6/0.01/0.02	–
Phacelia sericea	–	9.1/0.14/0.42
Poa alpina	7.9/0.14/0.39	–
P. pattersonii	15.8/0.24/0.95	40.9/3.59/22.96
Polemonium viscosum	18.4/0.58/2.49	4.5/0.68/1.44
Salix arctica	–	9.1/1.82/5.49
Selaginella densa	–	4.5/0.68/1.44
Senecio fremontii	23.7/0.12/0.58	–
Silene acaulis	2.6/0.39/0.63	4.5/1.70/3.61
Solidago multiradiata	5.3/0.08/0.18	31.8/0.43/2.42
Taraxacum lyratum	5.3/0.03/0.07	–
T. officinale	10.5/0.05/0.16	22.7/0.11/0.52
Townsendia montana	7.9/0.14/0.39	–
Trisetum spicatum	7.9/0.14/0.39	9.1/0.14/0.42
Unknown grasses	42.1/0.70/4.54	27.3/1.64/8.57
Unknown herbs	18.4/0.09/0.39	50.0/4.36/30.83

port the conclusions drawn from the transect data. Only a few species, such as *Poa pattersonii, Agropyron caninum,* and *Taraxacum officinale,* appear to be equally common in both areas. Furthermore, a group of species appears to be restricted to an area at the base of the distal moraine slope. They are found in a band ranging from 1 m up to 10 m wide between the moraine slope and the meadow proper. This band is formed primarily of debris derived from slumping and sliding off the distal moraine slope. Some of the species that were found in this ecotonal region include *Anemone multifida, Draba lonchocarpa, Oxytropis deflexa, Taraxacum lyratum, Androsace septentrionalis, Castilleja sulphurea,* and *Eritrichium nanum.* Few of these species were found on the moraine, and they were all either rare or absent from the meadow. The transect data show that this ecotonal region is richer in species than either the moraine or meadow. Average number of species per quadrat ranged from 4 on the moraine, to 5.1 in the meadow, to 7.3 in the ecotone between the two.

Using prominence values (PV), the most important species on the moraine are *Cirsium tweedyi, Epilobium alpinum, Polemonium viscosum, Agropyron caninum,* and *Poa pattersonii.* In the meadow the most important species are *Astragalus kentrophyta, Hymenoxys grandiflora, Antennaria umbrinella, Poa pattersonii,* and *Agropyron caninum.* Using the contribution of each species PV to the total summed PV for the moraine and the meadow, dominance diversity curves can be constructed (Fig. 3). Both curves approach geometric series, which have been suggested to indicate harsh environments in which dominance by one or a few species is strong (Whittaker 1975). On the moraine, several species share dominance; these are *Cirsium tweedyi* (28 percent of the total summed PV's), *Epilobium alpinum* (16 percent), *Polemonium viscosum* (15 percent), and *Agropyron caninum* (10 percent). In the meadow, *Astragalus kentrophyta* dominates (63 percent). Other species include *Hymenoxys grandiflora* (10 percent), *Antennaria umbrinella* (9 percent), and *Poa pattersonii* (6 percent). Of the eight species listed above, the majority are either western North American alpine species (*P. viscosum, A. kentrophyta,*

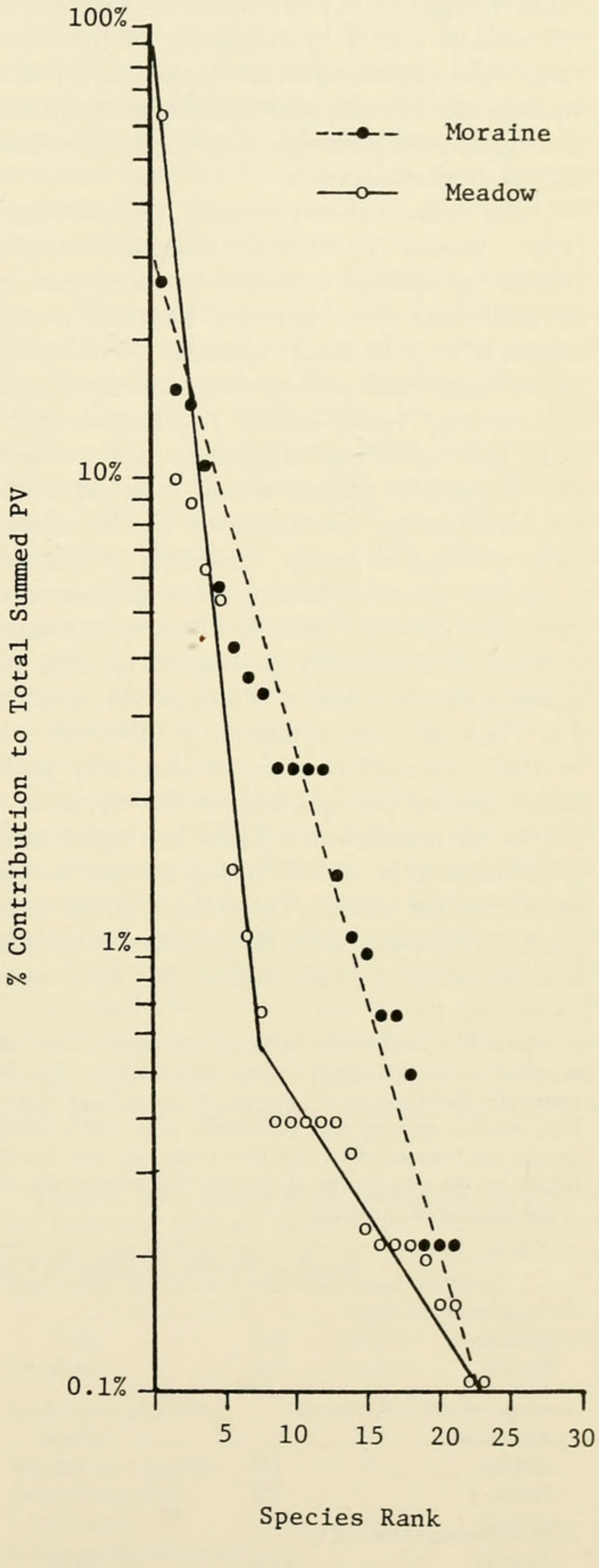

Fig. 3. Dominance-diversity curves for the moraine and the meadow. The measure of importance used was each species contribution to the total summed prominence values in percent. There are 21 species in the moraine curve and 23 species in the meadow curve. All species with values less than 0.1 percent had 0.1 percent added to their value to include them on the graph. This tended to slightly flatten the two curves at the bottom.

P. pattersonii, and *A. umbrinella*) or south/central Rocky Mountain alpine species (*C. tweedyi* and *H. grandiflora*). Of the other two, *Epilobium alpinum* (sensu lato) is a widespread circumpolar arctic-alpine species and *Agropyron caninum* is a North American boreal-montane species.

Using information derived from Fryxell (1957), Swales (1979), and Ostler and Harper (1978), the species from the transects can be divided into two groups, biotically and abiotically pollinated species. Wind-pollinated, suspected autogamous and apomictic species (i.e., *Arabis lyallii, Taraxacum officinale,* and *Epilobium alpinum*), and the fern ally *Selaginella densa,* which requires water for fertilization, are included in the abiotically pollinated group. Biotically pollinated (primarily entomophilous) dicot species comprise the biotically pollinated group. Average number of abiotically pollinated species per quadrat on the moraine is 1.0, in the meadow 1.4. These are not significantly different at $\alpha = 0.05$. Average number of biotically pollinated species per quadrat on the moraine is 1.2, in the meadow 3.1. These are significantly different at $\alpha = 0.05$ (using a t-test for unequal sample sizes). These and other comparisons between these two groups of species are summarized in Table 2. The total summed PV for all the moraine species in the abiotically and biotically pollinated groups are 11.0 and 6.4, respectively. For the meadow they are 54.9 and 343.9, respectively. The ratio of PV for the abiotically pollinated species in the meadow and the moraine is 5:1, and that for the biotically pollinated species is 53:1. The total number of species on the moraine and in the meadow for the abiotically pollinated group are 8 and 9, respectively. For the biotically pollinated group the values for the moraine and meadow are 13 and 14, respectively. All these comparisons suggest that the species in the abiotically pollinated group are relatively more succesful at colonizing and establishing on the moraine deposits than the species in the biotically pollinated group. The reverse is true for the meadow, where the biotically pollinated species dominate. There could be several reasons for these differences. Perhaps the open nature of the vegetation on the moraine makes it more difficult for biotically pollinated species to attract pollinators. Thus species that are autogamous, apomictic, or anemophilous may be at a reproductive advantage. It is also possible that such breeding systems are linked with other traits that confer greater colonizing abilities than is found in the biotically pollinated species (Jain 1976). Differential dispersion of propagules onto the moraine by species in the two categories does not appear to be the reason (see below).

Table 2. Comparisons between the moraine and the meadow using the quadrat data derived from the line transects. Two groups of species, abiotically pollinated (the abiotic group) and biotically pollinated (biotic group) are compared for the two areas. See the text for details on the two groups of species. The sample size (N) is the number of quadrats.

	Moraine (N = 38)	Meadow (N = 22)
Average percent cover		
Abiotic	2.5	10.7
Biotic	3.0	44.5
Average number of species per quadrat		
Abiotic	1.0	1.4
Biotic	1.2	3.1
Σ Prominance values (PV)		
Abiotic	11.0	54.9
Biotic	6.4	343.1
Number of species		
Abiotic	8	9
Biotic	13	14
Total number of species		
Abiotic	12	
Biotic	19	

Turning to the propagule trapping results, the water trays caught only five propagules during several weeks of operation. The water in the trays tended to evaporate quickly, and many propagules were probably blown out of the trays once they had dried out. These five propagules and those trapped by the petroleum-jelly-coated wooden plates used in 1979 are listed in Table 3. No propagules were trapped by the wooden plates in July, presumably because the plants were still flowering and had yet to set seed. In September, the trap furthest out into the meadow (30 m) trapped 23 propagules over a 24-hour period. The only other trap that caught anything was placed on the distal moraine slope in about midslope position. This trap caught a single unidentifiable composite achene with a pappus. Extrapolating from the data on number of propagules trapped and the size of the plates, the 23 propagules trapped in the meadow represent about 1022 propagules dispersing into and through every 1 m^2 every 24 hours, at a time in September when most species had finished flowering and were dispersing propagules. The calculated value for the trap on the moraine is 45 propagules per 1 m^2 per 24 hours, assuming that the single propagule trapped is representative of the propagule rain on the deposits. Most of the propagules (90 percent) have some morphological feature that might aid in more efficient wind dispersal. Such features include the coma of the Salix and Epilobium seeds and the pappus of the composite achenes. Two propagules, the Carex achene and the *Astragalus kentrophyta* legume, have no apparent features that could enhance wind dispersal ability. The propagule of *Geum rossii* represents a special case. This species is the only one that did not occur in the vicinity of the moraine or meadow. The propagule consists of a persistent calyx with numerous stiff hairs, enclosing many small achene fruits. It was found in one of the water trays in 1978, which raises the possibility that the propagule could have accidently dropped into the water from the fur of an investigating pika. Pikas are known to collect plants of *Geum rossii* for their hay piles (Johnson 1967). All the propagules trapped consist of dicot species except for the achene of the Carex species.

The moraine deposits appear to be in an active state of collapse. Fresh slumps and old slump scars can be found on both slopes, and are especially common on the proximal slope. The deposits are very loose and tend to shift easily underfoot. Numerous small erosion channels (rills) exist, attesting to the effects of snow meltwater erosion. The steepness of the slopes, which are from 36° to 38° on the distal slope and 35° to 41° on the proximal, contributes to the instability of the moraine. The combination of continual disturbance and apparently low rates of dispersal of propagules from the meadow is the probable explanation for the low average vegetation cover on the moraine slopes. The only portions of the moraine where the plant cover is as dense as in the meadow is along the crest, which in places is flat and presumably more stable than the steep slopes. The patches of vegetation on the flat portions of the crest are very similar to the meadow vegetation, including the presence of the three most common meadow species, *Astragalus kentrophyta, Hymenoxys grandiflora,* and *Antennaria umbrinella.* This suggests that, as the moraine deposits stabilize, they will become vegetated by the species that dominate and characterize the meadow.

A perusal of alpine vegetation literature from the south central Rocky Mountains failed to reveal any reports of vegetation similar to that found in the meadow (Rydberg 1914, Cox 1933, Cain 1943, Hayward 1952, Ellison 1954, Langenheim 1962, Johnson and Billings 1962, Bamberg and Major 1968, Habeck 1969, Bonham and Ward 1970, Lewis 1970, Anderson et al. 1979, Komarkova 1979), although many of the species in the meadow are common and widespread in the Rocky Mountains. On the other hand, several reports list vegetation that is strongly similar to that of the moraine (Buttars 1914, Mahaney 1974, Given and Soper 1975). In a detailed study from the Colorado Front Range, Komarkova (1979) listed several species that are characteristic of scree, talus, and glacial deposits (her Order Aquilegio-Cirsietalia scopulorum). Many of these species are also found at the Schoolroom Glacier moraine. These include *Senecio fremontii, Poa pattersonii, Oxyria digyna, Draba lonchocarpa, Epilobium alpinum, Taraxacum officinale,* and *Trisetum spicatum.* The thistle *Cirsium*

TABLE 3. The identity of the propagules trapped during 1978 and 1979 are listed, along with the number caught, and the presence of any morphological feature that might aid in more efficient wind dispersal.

Species	Number trapped	Morphological feature
Epilobium alpinum (seeds)	8	coma
Salix arctica (seeds)	9	coma
Arnica longifolia (achenes)	3	pappus
Geum rossii (achenes enclosed in calyx)	1	hairy calyx
Solidago multiradiata (achene)	1	pappus
Astragalus kentrophyta (legume)	1	–
Carex species (achene)	1	–
Unknown composites (achenes)	5	pappus

scopulorum appears to play an ecological role similar to *Cirsium tweedyi* in the Tetons.

In summary, the vegetation on the Schoolroom Glacier moraine is very open, with average cover ranging from less than 1 percent up to 9 percent, compared with over 50 percent in the alpine dry meadow adjacent to it. Dominance-diversity curves using prominence values as the measure of importance were constructed for the meadow and the moraine. Both curves approach geometric series, suggesting harsh environments in which dominance by one or a few species is strong. The legume *Astragalus kentrophyta* dominates the meadow, and the thistle *Cirsium tweedyi* dominates the moraine. Using cover and frequency data, abiotically pollinated species are relatively much more successful on the moraine than biotically pollinated species. The reverse is true in the meadow. Propagule trapping studies suggest that wind dispersal onto the moraine is very low compared with wind dispersal within the meadow. Distributionally, three groups of species can be discerned. One group is concentrated primarily on the moraine, only rarely straying into the meadow. The second group is found primarily in the meadow. The third group consists of species that are found in a narrow band between the base of the distal moraine slope and the meadow. This band of vegetation has many of the characteristic of an ecotone. The moraine deposits are highly unstable, and, in the few places along the crest of the moraine that tend to be the most stable, the vegetation is strongly similar to the vegetation in the meadow.

Acknowledgments

This paper represents partial requirements for a M.Sc. thesis by JRS, under the supervision of RJS. We thank the National Park Service, particularly Linda Olson and Bob Wood, for collecting permits and for other help.

Literature Cited

Anderson, D. C., R. S. Hoffman, and K. B. Armitage. 1979. Aboveground productivity and floristic structure of a high subalpine herbaceous meadow. Arctic and Alpine Res. 11:467–476.

Bamberg, S. A., and J. Major. 1968. Ecology of the vegetation and soils associated with calcareous parent materials in three alpine regions of Montana. Ecol. Monogr. 38:127–167.

Bonham, C. D., and R. T. Ward. 1970. Phytosociological relationships in alpine tufted hairgrass (*Deschampsia caespitosa* [L.] Beauv.) meadows. Arctic and Alpine Res. 2:267–275.

Buttars, F. K. 1914. Some peculiar cases of plant distribution in the Selkirk Mountains, British Columbia. Minnesota Bot. Studies 4:313–331.

Cain, S. A. 1943. Sample-plot technique applied to alpine vegetation in Wyoming. Amer. J. Bot. 30:240–247.

Cole, F. 1975. Introduction to meterology. 2d ed. Wiley & Sons, New York.

Cox, C. F. 1933. Alpine plant succession on James Peak, Colorado. Ecol. Monogr. 3:300–372.

Ellison, L. 1954. Subalpine vegetation of the Wasatch Plateau, Utah. Ecol. Monogr. 24:89–184.

Fryxell, P. A. 1957. Mode of reproduction of higher plants. Botanical Rev. 23:135–233.

Given, D. R., and J. H. Soper. 1975. Pioneer vegetation on moraines near Clachnacudainn Snowfield, British Columbia. Syesis 8:349–354.

Habeck, J. R. 1969. A gradient analysis of a timberline zone at Logan Pass, Glacier Park, Montana. Northwest Sci. 43:65–73.

Hayward, C. L. 1952. Alpine biotic communities of the Uinta Mountains, Utah. Ecol. Monogr. 22:93–120.

Jain, S. K. 1976. The evolution of inbreeding in plants. Ann. Rev. Ecol. Syst. 7:469–495.

Johnson, D. R. 1967. Diet and reproduction of Colorado pikas. J. Mammol. 48:311–315.

Johnson, P. L., and W. D. Billings. 1962. The alpine vegetation of the Beartooth Plateau in relation to cryopedogenic processes and patterns. Ecol. Monogr. 32:105–135.

Komarkova, V. 1979. Alpine vegetation of the Indian Peaks Area, Front Range, Colorado Rocky Mountains. Flora et Vegetatio Mundi, 7. R. Tüxen, ed. Cramer, Vaduz.

Langenheim, J. H. 1962. Vegetation and environmental patterns in the Crested Butte area, Gunnison County, Colorado. Ecol. Monogr. 32:249–285.

Lewis, M. E. 1970. Alpine rangelands of the Uinta Mountains. U.S. Forest Service—Region 4.

Love, J. D., and J. C. Reed. 1968. Creation of the Teton Landscape. Grand Teton Natural Hist. Assoc. Press.

Mahaney, W. C. 1974. Soil stratigraphy and genesis of Neoglacial deposits in the Arapaho and Henderson cirques, central Colorado Front Range. Geogr. Monogr. 5:197–240.

———. 1975. Soils of post-Audubon age, Teton Glacier area, Wyoming. Arctic and Alpine Res. 7:141–153.

Mahaney, W. C., and J. R. Spence. 1983. Late Quaternary deposits, soils, chronology, and floristics, Jaw Cirque area, Central Teton Range, Wyoming. In preparation.

Ostler, W. K., and K. T. Harper. 1978. Floral ecology in relation to plant species diversity in the Wasatch Mountains of Utah. Ecology 59:848–861.