

# Natural Regeneration of Alpine Tundra Vegetation after Human Trampling: a 42-year Data Set from Rocky Mountain National Park, Colorado, U.S.A.

Beatrice E. Willard\*

David J. Cooper† and

Bruce C. Forbes‡

\*Deceased

†Department of Forest, Rangeland and Watershed Stewardship, Colorado State University, Fort Collins, Colorado 80523, U.S.A.

DavidC@cnr.colostate.edu

‡Arctic Centre, University of Lapland, Box 122, FIN-96101 Rovaniemi, Finland.

BForbes@ulapland.fi

## Abstract

The vegetation composition of four contiguous permanent plots was analyzed during 37 of 42 years between 1959 and 2001 to evaluate successional processes following the cessation of human trampling in alpine tundra. The plots were established adjacent to the Rock Cut parking lot at ~3658 m elevation along Trail Ridge Road in Rocky Mountain National Park, Colorado. Due to limitations in the original study design, the lack of true replication required that the plots be treated individually when subject to indirect ordination analysis to follow trends in overall plant composition and cover. The three most abundant species in the study plots were *Artemisia scopulorum*, *Acomastylis rossii*, and *Kobresia myosuroides*. At the beginning of the study in 1959, total cover ranged from 20 to 55% in the four plots. By 1961, three of the four plots achieved total canopy cover values of at least 100%. Vascular plant species richness (number of taxa per plot) averaged 20 in 1959, but by 1967 had nearly doubled to 37. During the first several years, rates of seedling emergence were high among most taxa with the notable exceptions of *K. myosuroides* and *A. rossii*. However, likely due to desiccation and needle ice, seedling mortality was high. *K. myosuroides* spread exclusively from remnant tufts, as did three species of cushion plants which survived the trampling. The overall decline in plant cover during the last two decades of this study, particularly for *K. myosuroides*, indicates that long-term unassisted regeneration of severely degraded alpine tundra sites will take more than a century. While there have been periods of plant colonization and spread, climate factors such as a series of heavy snow years, and unchecked soil erosion from trails, can limit plant establishment and stop the recovery process, or push the recovery back by several decades. The negative influence of soil erosion, and quite possibly additional trampling, over a significant portion of the study plot points to the critical importance of using extreme care when establishing long-term monitoring plots, particularly in high-use areas.

## Introduction

Recreation impacts are increasing in a variety of ecosystems around the world (Liddle, 1997). Ironically, pressures are often highest within so-called protected areas, particularly those within reasonable driving distance of large urban centers (Darling and Eichorn, 1967; Edwards, 1967; Ceballos-Lascuráin, 1996). Conlin and Ebersole (2001) reported that attempts to climb peaks over 4267 m (14,000 feet) high increased 300% in the Collegiate Peaks region of Colorado during the period 1990–2000. More than 1 million people travel over Trail Ridge Road in Rocky Mountain National Park each year with many stopping to hike in the alpine tundra. Alpine tundra ecosystems have long been considered sensitive because of a combination of factors: short growing season; vegetation dominated by slow-growing, long-lived perennials; irregular diaspore production; and shallow, readily erodible soils (Dotzenko et al., 1967; Willard and Marr, 1970; Bayfield, 1971; Ketchledge, 1971; Billings, 1973).

Since restoration of even relatively small disturbances is labor intensive in alpine areas, and seeding is only successful in sites with relatively moderate environmental conditions for wind exposure, water availability, and winter snow depth (Chambers, 1997), there is

a need to understand natural recovery potential. While short-term studies may be adequate for many low-elevation situations, a longer period of observation for both natural and assisted revegetation is necessary due to slow-growing alpine tundra plants. Already in the early stages of this study, the senior author estimated that the time to “rebuild a natural and persistent ecosystem” might be centuries (Willard and Marr, 1971). Unfortunately, few studies in any ecosystem have followed vegetation responses beyond the cessation of pedestrian trampling for more than one to three years. One study resampled New England forest vegetation five years after trampling (Kuss and Hall, 1991), another study repeatedly sampled Scottish montane heath during a period of eight years (Bayfield, 1979), and yet another study repeatedly sampled three different alpine vegetation types in Norway during 22 years (Wielgolaski, 1998; see also Coker et al., 1998).

The goal of this paper is to summarize 42 years of data monitoring the responses of alpine vascular flora and vegetation to protection from pedestrian trampling. Although the design is unorthodox by contemporary standards, and the data are derived from a small group of plots in one area, we know of no other study which has followed naturally regenerating alpine vegetation in detail over such a long time period.

## Study Sites and Methods

The study plots are situated adjacent to the Rock Cut overlook parking lot along Trail Ridge Road in Colorado's Rocky Mountain National Park at an elevation of ~3658 m (Willard and Marr, 1971). The road was completed in July 1932, and the parking lot was built during that period. At the time the plots were established, the main impact to the terrain adjoining the site of the contemporary parking lot was derived from unrestricted pedestrian trampling for a period of 26 years (1960 photo, Fig. 5a). The prevailing undisturbed vegetation is assumed to be similar to that which existed prior to trampling, based on the intact patches of plant cover at the commencement of the study. The Rock Cut plots are within a stand of the *Thalictrum alpinum*-*Kobresia myosuroides* association (Willard, 1979).

The Rock Cut enclosure has a 15° slope to the southeast. The ground was unevenly trampled, with erosion evident in some portions of the plots but not others, and a trail is apparent. The single sample area was subdivided into four plots, according to the visible level of disturbance intensity. The northwest quarter was primarily bare soil, with the A horizon exposed (impact degree 4; ecosystem radically altered by visitor impact; vegetation cover = 5–25% of natural) (Willard and Marr, 1970, 1971). The southwest quarter had several patches of bare B and C soil horizons (impact degree 5; ecosystem virtually destroyed by visitor impact; vegetation cover 0–5% of natural), whereas the other quarters had more plant cover, making them representative of impact degrees 2 (ecosystem obviously affected by visitor impact but vegetation cover = 85–90% of natural) and 3 (ecosystem definitely altered by visitor impact; total vegetation cover = 25–85% of natural). The plot size, 2 m<sup>2</sup>, was chosen to exceed the minimum area recommended for floristic classification according to the methods of Braun-Blanquet (1932).

Steel railing enclosures were established in the spring of 1972 to prevent pedestrian access and allow for natural regeneration of the vegetation. It is understood that actions taken to discourage hikers from using specific research areas are not always effective (e.g., Sutter et al., 1993). Given the location of the plot next to one of the most popular parking areas and trails along Trail Ridge Road, we can reasonably assume that visitors occasionally have at least lightly disturbed the plots over the years.

For the first four years of the study, summarized by Willard and Marr (1971), population level observations were made weekly during the snow-free season. These included mapping individual plants, counting seedlings per 5 dm<sup>2</sup>, and mapping and photographing the vegetation in detail. Community level measurements were made during the peak of the growing season, mid-July to mid-August, using Braun-Blanquet cover classes for each species. The cover classes were: 1 = 0–5%, 2 = 5–25%, 3 = 25–50%, 4 = 50–75%, and 5 = 75–100%. Each cover class was modified by subdivision into three categories. For example cover class 3 was subdivided into 3–, 3, and 3+ to include plants with cover of 25–33, 34–42, and 43–50% cover. No control plots were established. The senior author repeated these measurements annually until 1998 (data were not collected in 1966, 1977, 1981, and 1987). In 2001 field sampling was done by Cooper and Forbes.

Raw plant community data sets were ordinated using detrended correspondence analysis (DCA) using the program PC-ORD 4.14 (McCune and Meford, 1999) to identify overall patterns in vegetation composition change over time. The data were analyzed in four separate blocks corresponding to the four plots.

Climate data from nearby sites are available as follows: maximum snow pack on 1 May from the Lake Irene SNOTEL station (CO05J10S, elevation 3260 m), located 3 km west of the

study site in subalpine forest; growing season temperature and precipitation from the University of Colorado LTER Niwot Ridge site D-1 (<http://culter.colorado.edu/NWT/>), located 32 km south of the study area and at a similar elevation (3739 m). Precipitation data from station C-1 was used for June 1976, 1977, and 1980, and July 1976 because it was not collected at D-1 during those periods. C-1 is located at 3022 m elevation, just east of D-1 on Niwot Ridge.

## Results

### CLIMATE

Snowpack water equivalent (SWE) for the Lake Irene snow course on 1 May ranged from <20 to >100 cm for the years 1959–2001 (Fig. 1A). While this site is below treeline, it is indicative of the amount of precipitation received annually. Years with the lowest SWE were 1966, 1977, 1981, 1987, and during the period 1987–1992, indicating that a relatively small volume of water recharged soils during these years. Snowfall was highest during the period from 1978 to 1986, indicating a deep spring snowpack, a large volume of soil water recharge, and more snow to melt before the growing season began.

Summer precipitation varied during the study period (Fig. 1C). The years with the greatest summer precipitation were 1961, 1963, 1965, 1972, 1983–85, 1998, and 1999. The period with the least summer precipitation was 1975–1982, and the year with the least precipitation was 1985. Mean June temperature, which is indicative of early season growing conditions, was very cool in the period from 1982 to 1984, and very warm in many years from 1987 to the end of the study period (Fig. 1B).

### TOTAL PLANT CANOPY COVER

At the beginning of the study in 1959, total plant canopy cover ranged from 20 to 55% in the four plots. By 1961, three of the four plots achieved cover values of at least 100%. Two of these plots achieved values of >150%, having started with relatively high cover of 45 to 55%. Several species reached their peak cover values within the first five years, but then declined rapidly and most were subsequently present only in trace amounts. From 1961 to the early 1980s, a series of peaks and troughs in total plant cover were generally synchronous among all four plots (Fig. 1D). By the mid-1980s, a general decrease in overall cover began and continued through 2001, the time of the last sampling. In 2001 total cover in the four plots ranged from 5.7 to 60.6%.

### SPECIES RICHNESS

Vascular plant species richness (number of taxa per plot) averaged 20 in 1959 but by 1967 had reached nearly 37 (Fig. 1D). From 1965 to 1998 species richness averaged 35, although there is significant variance among years. For individual plots within a given year the range during this same period is 23 to 42 taxa.

### SPECIES ABUNDANCE

The three most abundant species in the study plots were *Artemisia scopulorum*, *Acomastylis rossii*, and *Kobresia myosuroides* (nomenclature follows Weber and Wittmann, 2001). *Artemisia scopulorum*, in the family Asteraceae, is a rhizomatous herbaceous dicot and had very low cover values at the onset, but increased significantly within the first few years, exceeding 10% by

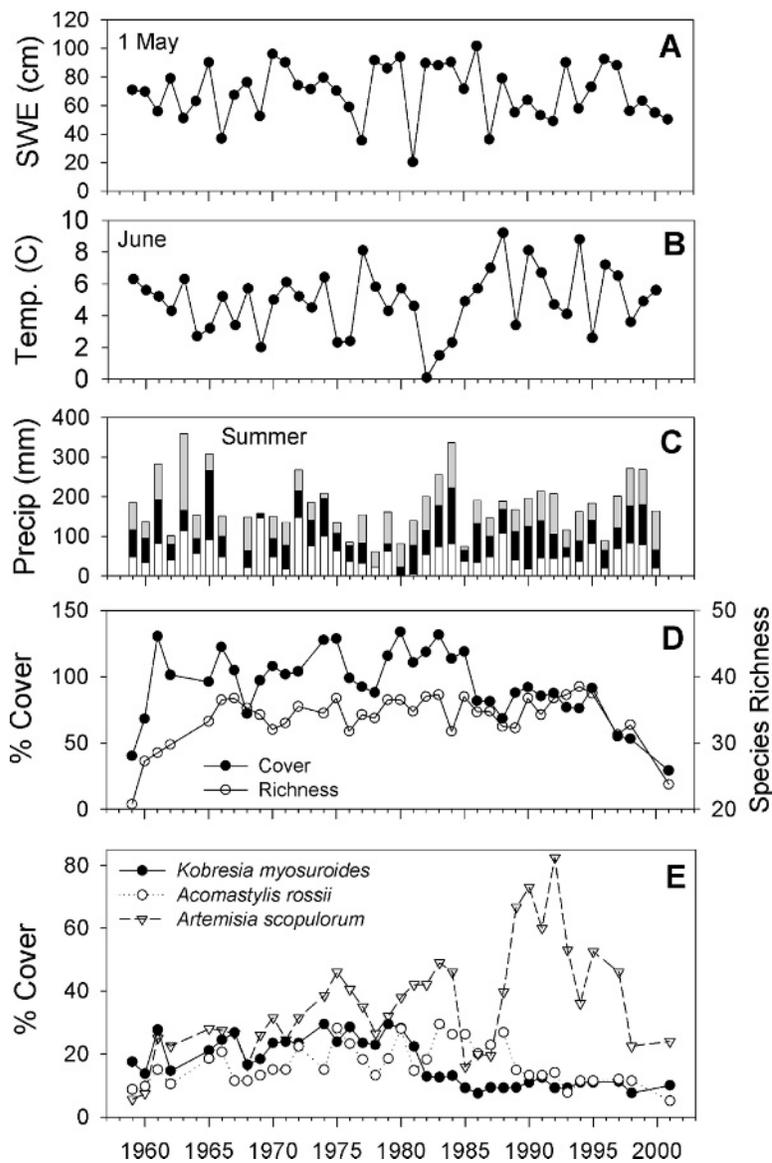


FIGURE 1. (A) Snowpack water equivalent (cm) from the Lake Irene snowcourse in Rocky Mountain National Park. (B) Mean June temperature at the Niwot Ridge D-1 station. (C) Summer precipitation for Niwot Ridge D-1 station. Stacked bars include June (white), July (black), and August (gray) totals. (D) Mean canopy cover and vascular plant richness for the four study plots. (E) Mean canopy cover for *Kobresia myosuroides*, *Acomastylis rossii*, and *Artemisia scopulorum* for the four study plots.

1961 in two plots (Fig. 1E). Cover of this species increased to >15% in all plots by the early 1990s, but had decreased again to an average of ~7% by 2001. Cover of *Acomastylis rossii*, a rhizomatous herbaceous dicot in the family Rosaceae, ranged from 4 to 15% in 1959, increasing through the 1960s and 1970s, and reaching an average of almost 40% in the mid 1980s. This species was dominant in the two western plots during most of the 42-year study period. However, by 2001 average cover was only 5%.

*Kobresia myosuroides* is a caespitose grass-like monocot in the family Cyperaceae and was dominant in the two eastern plots and had relatively high cover values of ~25% in 1959, whereas in the two western plots its cover ranged from 0 to 2.5%. In the two eastern plots, cover rose to an average of >45% by the late 1960s and reached a maximum in the mid 1970s of >50%. In the early 1980s cover began to decrease rapidly and by 1986 average cover was only 15%, less than it was in 1959. Since the early 1980s there has been no discernable recovery.

The majority of early colonizers were short-lived herbaceous dicotyledons and monocotyledons, and one moss species. Many of these species attained relatively high cover values in the first few years but quickly decreased to low cover, with some nearly absent

by 2001. This pattern is illustrated by *Oreoxis alpina*, *Festuca brachyphylla*, *Bryum argenteum*, and *Poa rupicola* (Fig. 2A). Other species such as *Castilleja occidentalis*, *Arenaria obtusiloba*, *Carex rupestris*, and *Sedum lanceolatum* follow the general pattern of *A. scopulorum* (Fig. 2B). *Carex rupestris* increased during the first years of the study, yet its cover varied widely from 1965–1984, after which its cover remained low. After consistent low cover during the first decades, *Castilleja occidentalis* increased to a relatively sudden peak of 15% in the southern two plots during the period 1988–1990, but then decreased to trace values by 1997. *Poa alpina* was not present in the early years, occurred at low cover values during the period 1965–1982, and then increased significantly starting in the early 1980s, coinciding with the decline of the three most abundant species described above. *Sedum lanceolatum* was also present in very low cover through the first 15 years of the study, and increased in 1975.

#### ORDINATIONS

Interpretation of the DCA analyses from all four plots was relatively straightforward and supports the general patterns described above for species richness, cover, and abundance. We

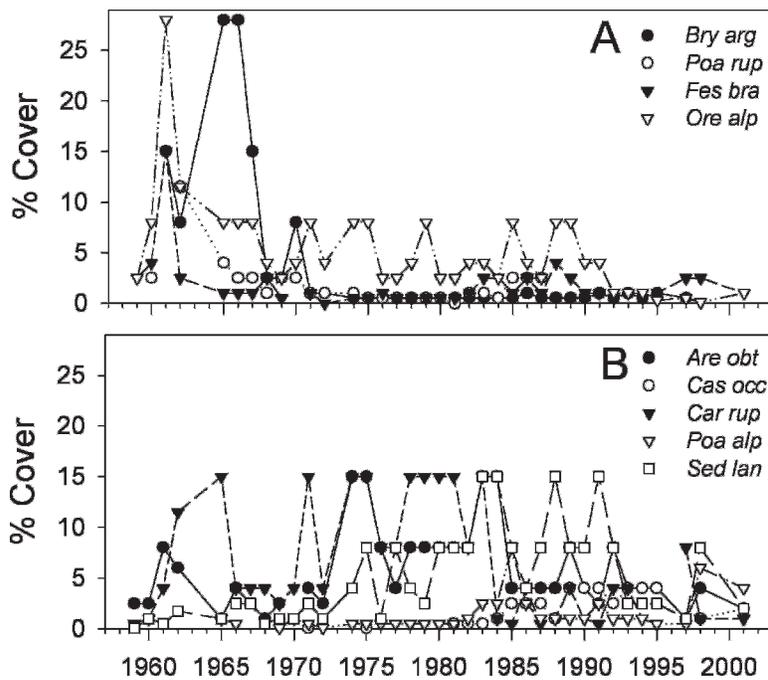


FIGURE 2. Mean canopy cover in the four study plots. (A) *Bryum argenteum* (*Bry arg*), *Poa rupicola* (*Poa rup*), *Festuca brachyphylla* (*Fes bra*), and *Oreoxis alpina* (*Ore alp*). (B) *Arenaria obtusiloba* (*Are obt*), *Castilleja occidentalis* (*Cas occ*), *Carex rupestris* (*Car rup*), *Poa alpina* (*Poa alp*), and *Sedum lanceolatum* (*Sed lan*).

chosed two plots, northeast (Fig. 3) and northwest (Fig. 4), to illustrate the overall trends in the vegetation during the study period. In all four plots, the early years after establishment of the enclosure were characterized by the rapid increase and decrease of many species that did not necessarily persist through the entire study period. This resulted in the scattering of these samples along the 2nd axis in the ordination space. In contrast, during much of the 1970s, the samples remain fairly well clustered toward the center of the plot, indicating relative stability in species composition and abundance throughout this period. The eastern and western plots behave somewhat differently during the 1980s and 1990s. In the northeast plot, the period 1982–1987 is represented by a new cluster of samples to the left of the plot center. The period 1988–2001 is represented by yet another, looser cluster of samples in the upper left portion of the ordination space. The western plots, as illustrated by the northwestern plot, are distinct because the years 1989–1993 form a cluster of samples to the right of the ordination center. In all cases, the final years of the

study (1998–2001) appear as outliers on the margins of the ordination space.

### Discussion

It is important to remember that in 1959, at the time the enclosures were established, the four plots were not homogeneous with regard to degree of impact and vegetation cover (Fig. 5). The northwest quarter was primarily bare soil with the A horizon visible, and the southwest quarter was characterized by several patches of bare B and C soil horizons. The eastern quarters both had relatively greater plant cover throughout the study period. Twenty-six vascular species had survived the trampling and had cover values ranging from a trace to >20%. *Kobresia myosuroides* was particularly abundant in the eastern plots and *Acomastylis rossii* in the western plots. Total species richness was higher in the eastern plots, nearly doubled in all plots between 1959 and 1967 (Fig. 1D), and then remained more or less stable through the rest

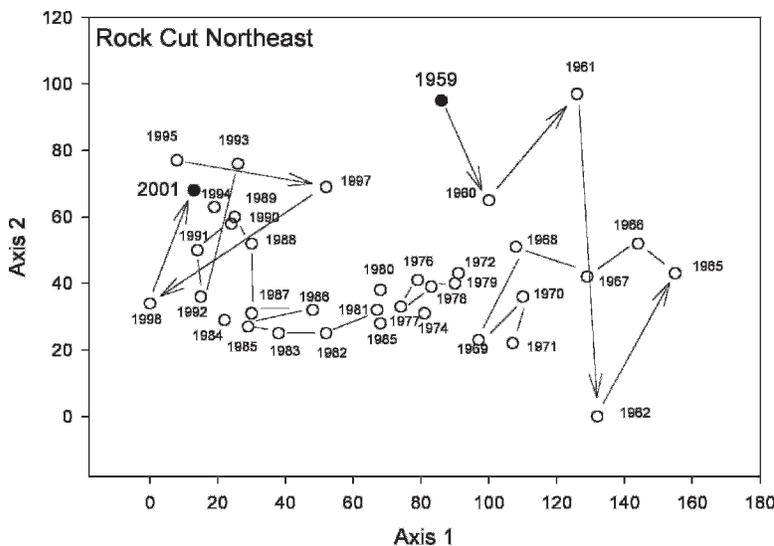


FIGURE 3. Detrended correspondence analysis (DCA) of vegetation composition for Rock Cut plot northeast for the years 1959–2001. Years are labeled, and arrows show the direction of change within the ordination space of axes 1 and 2.

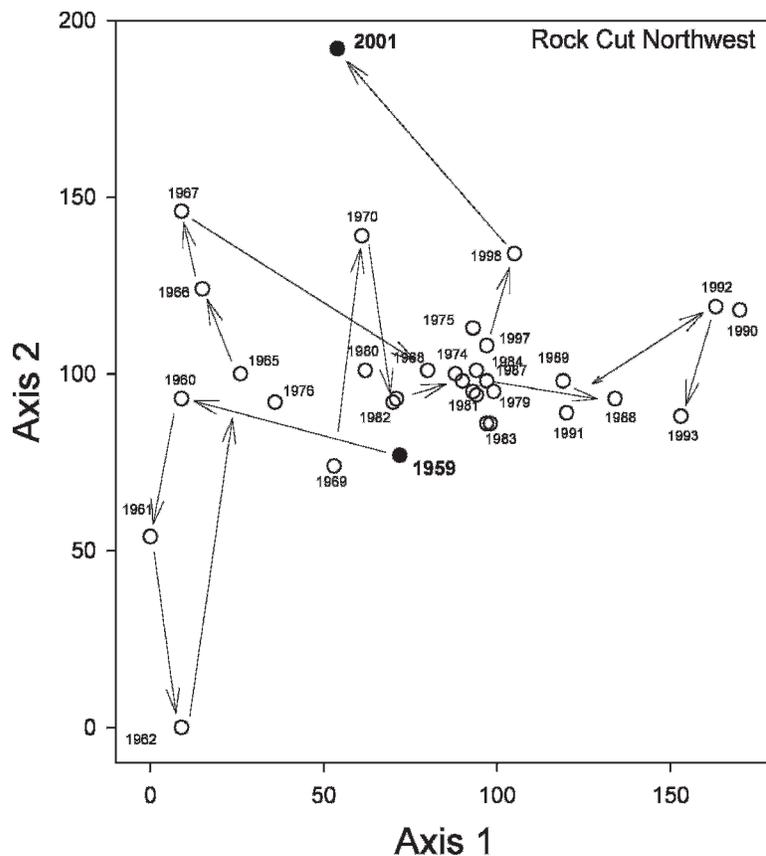


FIGURE 4. Detrended correspondence analysis (DCA) of vegetation composition for Rock Cut plot northwest for the years 1959–2001. Years are labeled, and arrows show the direction of change within the ordination space of axes 1 and 2.

of the study period. Canopy cover in 1959 ranged from 20 to 55%, but within three years had nearly tripled in all plots (Fig. 1D), with a maximum of 160% in the southeast plot.

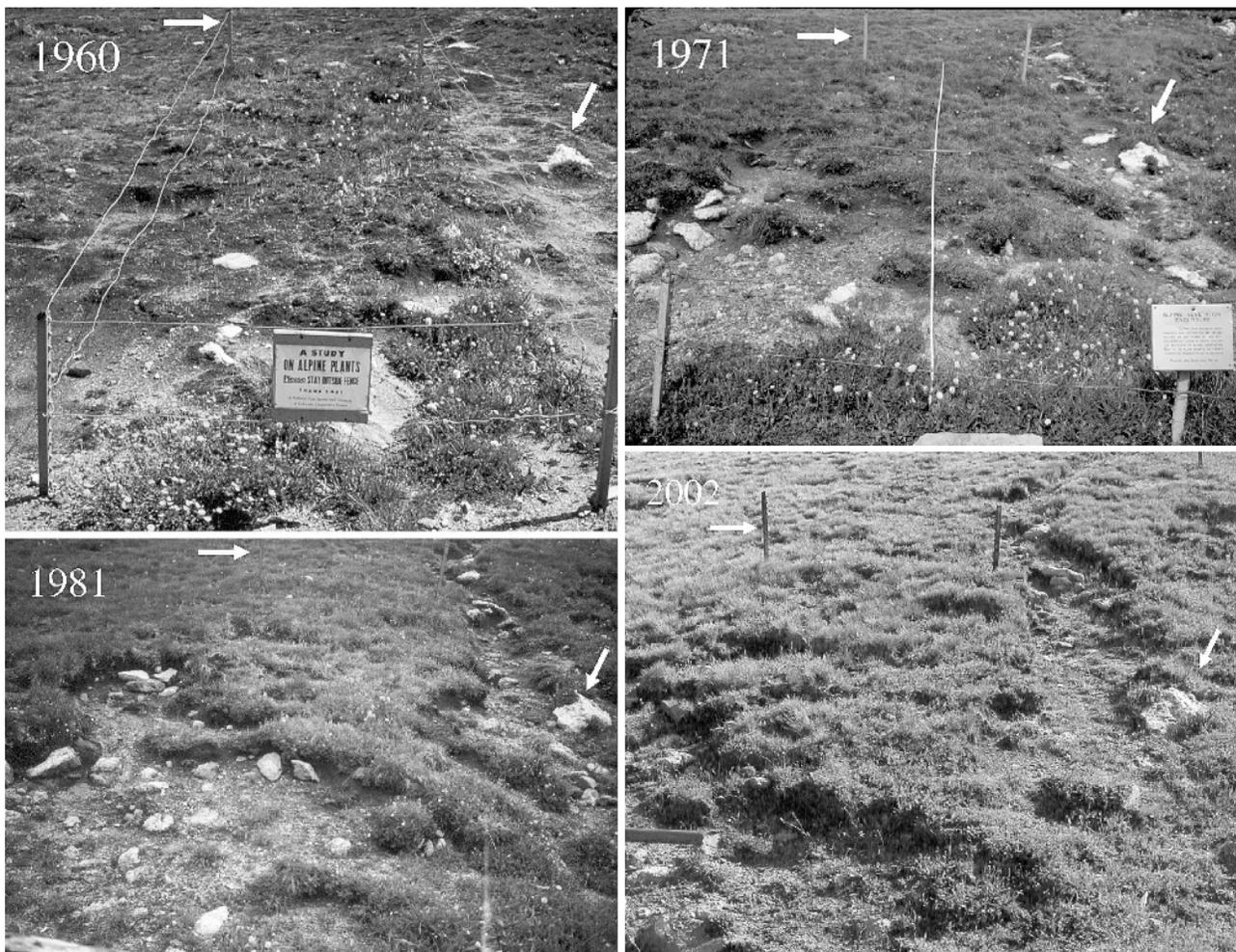
During the first several years, seedling emergence rates were high among most taxa with the notable exceptions of *Kobresia myosuroides* and *Acomastylis rossii*. Nor were seedlings of *Poa fendleriana* and *P. alpina* observed during the first four years (Willard and Marr, 1971). However, mortality of seedlings also appeared to be high, likely due to desiccation and needle ice (Raup, 1951; Churchill and Hanson, 1958), so that by autumn there was observable establishment among some taxa (e.g. *Polygonum bistortoides*, *Mertensia lanceolata*, and *Artemisia scopulorum*) but not others (e.g. *Trifolium nanum*, *Carex rupestris*, *Ranunculus pedatifidus*, and *Thalictrum alpinum*). *Kobresia myosuroides* spread exclusively from remnant tufts, as did three species of cushion plants which survived the trampling, *Silene acaulis*, *Minuartia obtusiloba*, and *Trifolium nanum*.

A number of species that were early colonists quickly contributed significantly to the total plant cover, including *Bryum argenteum*, *Oreoxis alpina*, *Poa rupicola*, and *Festuca brachyphylla* (Fig. 2A). However, by the beginning of the 1970s, some of the taxa with relatively high cover values in the early years had begun to decline to trace amounts (e.g. *Oreoxis alpina* and *Festuca brachyphylla*) or disappeared altogether (e.g. *Poa rupicola*) (Fig. 2A). All of these species had very low cover or were absent in 2001.

Taxa which increased in cover substantially during the 1970s included *Acomastylis rossii*, *K. myosuroides*, and *A. scopulorum* (Fig. 1E). By this time the total plant cover was stable enough to allow us to detect the impact of significant climatic episodes. For example, the winter of 1976–1977 was characterized by extremely low snowfall throughout the southern Rocky Mountains, ostensibly leading to early desiccation in the summer of 1977. This appears to

be reflected in our data set by the low canopy cover in all plots in 1977 and 1978 (Fig. 1D). This was followed by a period of high snow cover from 1978 to 1986, including several El Niño events that produced deep and late spring snow cover across Trail Ridge.

According to Bell (1974), *Kobresia bellardii* (All.) K. Koch (synonymous with *K. myosuroides* (Villars) Fiori & Paoli) (Weber and Wittmann, 1992) in the Colorado Front Range is physiologically well adapted to scant snow cover, profound temperature swings, and winter and summer desiccation, but is “extremely susceptible” (p. 152) to even brief burial beneath moderate to deep snow, as well as to grazing. Other studies have similarly documented rapid and extensive mortality among populations in the Colorado alpine subject to experimental snow augmentation (Webber et al., 1976; Walker et al., 1999). Snow cover might help explain why several species began to decline around 1980 following three successive springs with heavy snow cover (1978–1980). After one dry, cold spring/summer in 1981, the years 1982–1984 were again characterized by the aforementioned heavy snow accumulations. Although tussocks of *Kobresia* may persist and spread vegetatively for several hundred years, Bell and Bliss (1979) further suggested that once a population has begun to decline, natural regeneration would be difficult or impossible given its extremely low levels of seed production. On the other hand, while Ebersole (2002) confirmed that vegetative expansion was important on experimentally disturbed patches aged 13 years on Niwot Ridge, he also observed occasional colonization by seed in patches 31 years old. Nonetheless, it is clear that after 1981 *K. myosuroides* began to decline on the site, and it has yet to recover. Given the proximity to the parking lot, we cannot rule out additional stress on the population derived from further pedestrian access to the plots. The overall pattern of *Acomastylis rossii* cover during the study period was very similar to that of *Kobresia*, although its decline began in 1989, while *Kobresia*'s decline began in 1981.



**FIGURE 5.** Repeat photographs of the study plots for 1960, 1971, 1981, and 2002, looking north. The sizes of the four plots are indicated by the steel posts and wire in the 1960 photo; the outline of the four plots can be seen in the 1971 photo. The northwest corner post is identified with a white arrow in each photo, as is the location of a single rock that was in a severely eroded portion of the area. The yellow flowering plants visible, particularly in the 1960 and 1971 photos, are *Acomastylis rossii*.

Another species with a pronounced shift in cover over the course of the study is *Artemisia scopulorum* (Fig. 1E). Its cover increased from the study inception through 1975. Its cover then declined and later increased, reaching a second peak in 1983. It declined again in 1985, and later increased to its highest cover in 1992. According to Oberbauer and Billings (1981), this species displays significant drought tolerance, which may explain its considerable expansion during the relatively warm, dry years of the late 1980s and early 1990s. However, its cover has declined in recent years, and in 1999 it was no higher than in 1961 (Fig. 1E).

The overall decline in plant cover during the last two decades of this study, particularly for *Kobresia myosuroides*, indicates that unassisted regeneration of severely degraded alpine tundra sites is a long-term process. It is difficult to know the exact cause of the decline in plant cover reported here. While there have been periods of plant colonization and spread, ongoing erosion is a threat to the recovery of the original community unless the soils within the plots as well as upslope are stabilized to avoid the channeling of runoff. If such secondary disturbance is mitigated, recovery may occur relatively rapidly, but successional processes can also be influenced by climate factors such as a series of large snow years. The negative influence of soil erosion and quite possibly additional trampling over a significant portion of the study plots point to the critical importance of using extreme care when establishing long-

term monitoring plots, particularly in high-use areas. In future studies, true replication, as well as the establishment of control plots in undisturbed but comparable habitats of similar elevation, aspect, snow regime, and disturbance history would help to improve our understanding of decadal successional patterns and to partition autogenic from allogenic processes.

### Acknowledgments

This long-term study was permitted by Rocky Mountain National Park, and we appreciate their cooperation. The writing of this manuscript was made possible by funds from B. E. Willard.

### References Cited

- Bayfield, N. G., 1971: Some effects of walking and skiing on vegetation at Cairngorm. In Duffey, E., and Watt, A. S. (eds.), *The Scientific Management of Animal and Plant Communities for Conservation*. Oxford: Blackwell, 469–485.
- Bayfield, N. G., 1979: Recovery of four montane heath communities on Cairngorm, Scotland, from disturbance by trampling. *Biological Conservation*, 15: 165–179.
- Bell, K. L., 1974: Autecology of *Kobresia bellardii*: why winter snow accumulation patterns affect local distribution. Ph.D. thesis. University of Alberta: Edmonton, Canada.

- Bell, K. L., and Bliss, L. C., 1979: Autecology of *Kobresia bellardii*: why winter snow accumulation limits local distribution. *Ecological Monographs*, 49: 377–402.
- Billings, W. D., 1973: Arctic and alpine vegetations: similarities, differences, and susceptibility to disturbance. *BioScience*, 23: 697–704.
- Braun-Blanquet, J., 1932: *Plant Sociology: the Study of Plant Communities*. 1983 reprint. Koenigstein: Koeltz Scientific, 439 pp.
- Ceballos-Lascuráin, H., 1996: *Tourism, Ecotourism, and Protected Areas: the State of Nature-based Tourism around the World and Guidelines for its Development*. Gland: IUCN, 315 pp.
- Chambers, J. C., 1997: Restoring alpine ecosystems in the western United States: environmental constraints, disturbance characteristics and restoration success. In Urbanska, K., Webb, N., and Edwards, P. (eds.), *Restoration Ecology and Sustainable Development*. Cambridge: Cambridge University Press, 161–187.
- Churchill, E. D., and Hanson, H. C., 1958: The concept of climax in arctic and alpine vegetation. *Botanical Review*, 24: 127–191.
- Coker, P., Glaves, P., and Kent, M., 1998: Long-term recovery response of montane vegetation subject to recreational trampling. In Sjögren, E., van der Maarel, E., and Pokarzhevskaya, G. (eds.), *Vegetation Science in Retrospect and Perspective*. Abstracts. Uppsala: Opulus Press, 65 pp.
- Conlin, D. B., and Ebersole, J. J., 2001: Restoration of an alpine disturbance: differential success of species in turf transplants, Colorado, U.S.A. *Arctic, Antarctic, and Alpine Research*, 33: 340–347.
- Darling, F. F., and Eichorn, N. D., 1967: The ecological implications of tourism in national parks. *Proceedings IUCN*. New Series No. 7, Section 1/2.A.1: 112–115.
- Dotzenko, A. D., Papamichos, N. T., and Ramine, D. S., 1967: Effect of recreation use on soil and moisture conditions in Rocky Mountain National Park. *Journal of Soil and Water Conservation*, 22: 196–197.
- Ebersole, J. J., 2002: Recovery of alpine vegetation on small, denuded plots, Niwot Ridge, Colorado, U.S.A. *Arctic, Antarctic, and Alpine Research*, 34: 389–397.
- Edwards, R. Y., 1967: The impact of recreation on the landscape in the mountains of western Canada. *Proceedings IUCN*. New Series No. 7, Section 1/2.A.1: 124–126.
- Ketchledge, E. H., 1971: Facility rehabilitation. In Larson, E. (ed.), *The Forest Recreation Symposium*. Upper Darby, PA: U.S. Forest Service, 166–173.
- Kuss, F. R., and Hall, C. N., 1991: Ground flora trampling studies: five years after closure. *Environmental Management*, 15: 715–727.
- Liddle, M., 1997: *Recreation Ecology: the Ecological Impact of Outdoor Recreation and Ecotourism*. London: Chapman & Hall, 639 pp.
- McCune, B., and Meford, M. J., 1999: *PC-ORD. Multivariate Analysis of Ecological Data. version 4.0*. Gleneden Beach, OR: MjM Software Design, 47 pp.
- Oberbauer, S. F., and Billings, W. D., 1981: Drought tolerance and water use by plants along an alpine topographic gradient. *Oecologia*, 50: 325–331.
- Raup, H. M., 1951: Vegetation and cryoplanation. *Ohio Journal of Science*, 51: 105–116.
- Sutter, R. D., Benjamin, S. E., Murdock, N., and Teague, B., 1993: Monitoring the effectiveness of a boardwalk at protecting a low heath bald in the southern Appalachians. *Natural Areas Journal*, 13: 250–255.
- Walker, M. D., Walker, D. A., Welker, J. M., Arft, A. M., Bardsley, T., Brooks, P. D., Fahnestock, J. T., Jones, M. H., Losleben, M., Parsons, A. N., Seastedt, T. R., and Turner, P. L., 1999: Long-term experimental manipulation of winter snow regime and summer temperature in arctic and alpine tundra. *Hydrological Processes*, 13: 2315–2330.
- Webber, P. J., Emerick, J. C., Ebert-May, D. C., and Komárková, V., 1976: The impact of increased snowfall on alpine vegetation. In Steinhoff, H. W., and Ives, J. D. (eds.), *Ecological Impacts of Snowpack Augmentation in the San Juan Mountains, Colorado*. Denver: U.S. Department of the Interior, Bureau of Reclamation, 201–258.
- Weber, W. A., and Wittmann, R. C., 1992: *Catalog of the Colorado Flora: a Biodiversity Baseline*. Niwot: University Press of Colorado, 215 pp.
- Weber, W. A., and Wittmann, R. C., 2001: *Colorado Flora, Eastern Slope*. Third edition. Niwot: University Press of Colorado, 521 pp.
- Wielgolaski, F.-E., 1998: Twenty-two years of plant recovery after severe trampling by man through five years in three vegetation types at Hardangervidda. *Norges Teknisk-Naturvitenskapelige Universitet, Vitenskapsmuseet, Rapport Botanisk Serie*, 1998-4: 26–29.
- Willard, B. E., 1979: Plant sociology of alpine tundra, Trail Ridge, Rocky Mountain National Park, Colorado. *Colorado School of Mines Quarterly*, 74(4): 1–119.
- Willard, B. E., and Marr, J. W., 1970: Effects of human activities on alpine tundra ecosystems in Rocky Mountain National Park, Colorado. *Biological Conservation*, 2: 257–265.
- Willard, B. E., and Marr, J. W., 1971: Recovery of alpine tundra under protection after damage by human activities in the Rocky Mountains of Colorado. *Biological Conservation*, 3: 181–190.

*Ms accepted May 2006*