Recovery of Alpine Vegetation on Small, Denuded Plots, Niwot Ridge, Colorado, U.S.A.

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Abstract

Small plots (0.25 to 1.0 m²) denuded 13 and 31 yr previously were studied to investigate vegetation recovery at the alpine site of the Long-Term Ecological Research network. Recovery was slow, probably due to poor seedling survival. Covers of vascular plants and lichens were much lower on denuded plots than on controls except in late-melting snowbanks where natural disturbance by pocket gophers may have selected for disturbance-adapted species. Moister communities generally regained cover faster than drier communities. Vegetative expansion from plot edges provided most cover, although some colonizers originated from seed. *Kobresia myosuroides*, previously unknown to reproduce sexually in the Southern Rocky Mountains, occasionally colonized by seed. Essentially all vascular species acted as both colonizers and components of mature vegetation, and the vast majority of species are present in similar relative frequencies in control and disturbed plots. Previously studied alpine sites show either a similar lack of differentiation of early- and late-successional species or higher relative abundance of grasses in disturbed sites. In contrast to vegetation recovery in most temperate ecosystems, in these small plots on Niwot Ridge sequential replacement of species after disturbance does not occur.

Introduction

Whittaker (1974) and MacMahon (1980) generalized that succession is less obvious in alpine, arctic, and desert areas than in other terrestrial ecosystems. In the alpine, few studies exist that document changes in species composition through time after disturbance (used here to mean removal of plant cover). There is also limited information on differences in successional rates and patterns among the variety of plant communities within the alpine.

Two sets of experimentally denuded plots and appropriate controls on Niwot Ridge, alpine site of the Long-Term Ecological Research network, allowed this study. Plots denuded 13 yr prior to study existed in two communities on Niwot Ridge, and ca. 30-yr-old plots were present in four communities. Although spatial patterns of alpine vegetation on Niwot Ridge are well studied, little is known about temporal changes (Walker et al., 2001). In addition, information on how recovery rates and patterns vary among alpine plant communities can help prioritize vegetation restoration efforts in similar alpine areas (e.g., Hesse, 2000; Conlin and Ebersole, 2001; Ebersole et al., 2002).

The specific questions asked were (1) are some vascular plant species limited to or more common in early vs. late successional stages? and (2) are there differences in rates of recovery among four common Niwot Ridge plant communities?

Site Description

Niwot Ridge (40°03′N, 105°35′W) lies in the Colorado Front Range. It has a strongly continental climate and very windy and cold winters. A ridgetop site at 3750 m receives an average of 993 mm precipitation per year. Precipitation is highest in the winter and spring, and there is relatively little during the growing season and fall (Greenland and Losleben, 2001). Strong

westerly winter winds redistribute snow with some areas nearly snow-free and others melting out in midsummer (Komárková, 1979; Walker et al., 1993). Soil moisture varies greatly across the landscape depending on snow deposition as well as presence and duration of melting snowbanks.

Vegetation varies according to soil moisture and time of snowmelt. Fellfields dominated by cushion plants occupy ridgetops mostly blown free of snow in winter, and dry meadows dominated by *Kobresia myosuroides* cover slightly less wind-blown sites. (Botanical nomenclature follows the Natural Resources Conservation Service PLANTS database [USDA, NRCS, 2001].) Both communities have minimal snow cover in winter. Wet sedge meadows cover low areas and drainages. Snowbank communities occur on east-facing slopes where snowmelt occurs between early June and August depending on topographic location and snowfall of the previous winter (Komárková, 1979; May and Webber, 1982; Walker et al., 1993, 2001).

In 1994, I studied plots experimentally denuded of vegetation in September 1963 by W. S. Osburn (ca. 30-yr-old plots) and resampled by Phillips (1984). Half of these 50 cm × 50 cm plots had all plants, including underground structures, and the organic soil horizon removed in 1963 (Osburn, pers. comm., 1997; Phillips, 1984). Remaining undisturbed plots served as controls. These plots were used for a seedling survival study, and in the disturbed plots for the next ca. 8 yr, any sprouts from roots or rhizomes were removed as they appeared (Osburn, pers. comm., 1997). Sample size ranged from 2 to 3 within treatments (see Results).

Plots were in the following plant communities (for more complete community descriptions see Walker et al., 2001): (1) dry meadow (*Selaginello–Kobresietum myosuroidis* [all Braun-Blanquet equivalents are from Komárková, 1979]), (2) fellfield (*Sileno-Paronychietum*), and (3) late-melting snowbanks (*Toni-*

nio-Sibbaldietum). There were two sets of plots in the fellfield, a relatively typical example and a very xeric example of this dry community. The fellfield and late-melting snowbank communities were in or near the "Saddle" area of Niwot Ridge at approximately 3530 m, and the dry meadow was at the D1 climate station at 3750 m. All communities appeared quite stable, and Kooiman and Linhart (1986) showed that species composition of the dry meadow at D1 changed little in the 28 yr from 1953 to 1981.

Due to removal of the thick organic horizon of the dry meadow, surfaces of disturbed plots in this community were about 10 cm below the surrounding vegetation. Surfaces of disturbed plots in the other communities were even with the surrounding vegetation because there was no organic horizon to remove.

Plots disturbed in 1981 and associated control plots (Pollak et al., 1988) were also studied in 1994. Experimenters removed aboveground vegetation from disturbed plots, but, in contrast to the 30-yr-old plots, did not remove either the organic horizon or subsequent vegetative spouts. These 13-yr-old plots were 1 m × 1 m and arranged in a paired design with each disturbed plot about 20 cm from its control plot. These were in two communities in the Saddle: (1) dry meadow, and (2) moist meadow, which is an early-melting snowbank (*Stellario laetae–Deschampsietum caespitosae*). Originally there were 10 pairs of plots in each community (Pollak et al., 1988), but two pairs of plots in each community had undergone unknown additional treatments, so sample size for this study in each community was 8 pairs.

Methods

Frequency data for all vascular plant species were collected 29 July to 4 August 1994 using 0.5 × 0.5 m or 1 × 1 m frames divided with string into 10 × 10 cm squares. Frequency is commonly used for monitoring plant populations and is appropriate for life history types common on Niwot Ridge (Elzinga et al., 1998). For the 30-yr-old 50 cm × 50 cm plots, the 25 squares covering the entire plots were used. For the 13-yr-old 1 m × 1 m plots, every third square of nine rows (27 total) was used. To best sample potential spatial variation in the plots, I used squares 1, 4, and 7 of row one, squares 2, 5, and 8 of row two, squares 3, 6, and 9 of row three, etc. Species presence-absence data from the 10 cm × 10 cm squares were used to calculate absolute frequency of each vascular species for each plot. Relative frequencies were then calculated as the absolute frequency of each species divided by the sum of frequencies of all vascular species in that plot. Mean relative frequencies from disturbed versus control plots within each community and age were compared using *t*-tests. Thus, the tests do not compare absolute frequency since for almost all species this is less in disturbed plots. Instead, the tests ask whether each species comprises a relatively greater or smaller proportion of vegetation in disturbed plots compared to controls. I also visually estimated aerial cover by major taxonomic group (vascular plants, bryophytes, lichens) from projected slides of the plots and analyzed results with *t*-tests.

For the 13-yr-old plots, paired *t*-tests were used after determining that differences in relative frequencies between paired plots met the normality assumption. For the 30-yr-old plots, normality was also tested before applying random groups *t*-tests. Equality of variances was not tested since inequality of variances does not affect probability values when sample sizes are equal (Scheffé, 1959). I determined power of the tests with the computational methods of Zar (1984).

I measured volumetric soil moisture 4–6 August 1994 with time domain reflectometry (Taylor and Seastedt, 1994). This method provides an integrated measure of moisture in the top 15 cm of soil. The standard equation of Topp et al. (1980) was used to convert waveform distances to volumetric soil moisture. The 1.3 mm of rain that fell 6 August 1994 did not appear to affect measurements. All snow above plots had melted several weeks prior to measurement.

Soil nitrogen for each plot was determined from a composite of two cores 1.85 cm in diameter and 10 cm deep taken 1–4 August 1994. KCl-extractable NO_3^--N and NH_4^+-N were determined colorimetrically using a Lachat flow injection analyzer as described by Bowman et al. (1993). Soil moisture and nitrogen data were analyzed with *t*-tests as described for plant data.

Results

For the 13-yr-old plots, power of *t*-tests to distinguish between control and disturbed means was quite high except for large standard deviations. Power varied from 0.65 to 1.00 for the median standard deviation of relative frequencies and for true differences of 2 to 8 percentage points. This means lack of significant differences between control and disturbed relative frequencies and abiotic factors are likely real rather than artifacts of low statistical power. For the smaller sample sizes ($n = 2$ to 3) of the 30-yr-old plots, power for the median standard deviation ranged from 0.04 for $n = 2$ and differences of 2 percentage points to 0.93 for $n = 3$ and differences of 8. When true differences between means are small and/or standard deviations are large, a finding of no significant difference may be an artifact of small sample size rather than a true lack of difference. Thus, for the 30-yr-old plots, I interpreted statistical results more subjectively than usual.

For communities with differences in early August soil moisture between disturbed and control plots, the general pattern is that in drier communities disturbed plots were drier while in moister communities disturbed plots were moister (Fig. 1). In the 30-yr-old plots, moisture was more than 50% lower ($P < 0.08$) in disturbed plots than control plots in the typical fellfield and dry meadow (Fig. 1). Differences in soil moisture between disturbed and control plots were not different in the xeric fellfield and late-melting snowbank communities (Fig. 1). In the 13-yr-old experiment, disturbed and control plots were not different in soil moisture in the dry meadow, but soil moisture was about two times higher in disturbed plots in the moist meadow community.

Extractable nitrate was quite low in all communities, and there were no differences between control and disturbed plots in any of the communities (Fig. 1). For extractable ammonium, the two driest communities at this time of year, late-melting snowbank and xeric fellfield, showed no differences between disturbed and control plots. Moister communities have higher concentrations of extractable ammonium in control plots (except for the 13-yr-old dry meadow plots).

The vast majority of vascular plant taxa in both 13- and 30-yr-old Niwot Ridge plots occur with similar relative frequencies in control and disturbed plots (Tables 1, 2). There were 11 instances of taxa having greater relative frequency in control plots, 115 with no difference, and 8 cases of taxa with higher relative frequency in disturbed plots. The low power of tests for the 30-yr-old plots may affect these summary statistics somewhat since it is more difficult to detect differences between means of control and disturbed plots. Results from the dry meadow probably illustrate this difference in power between the 13-
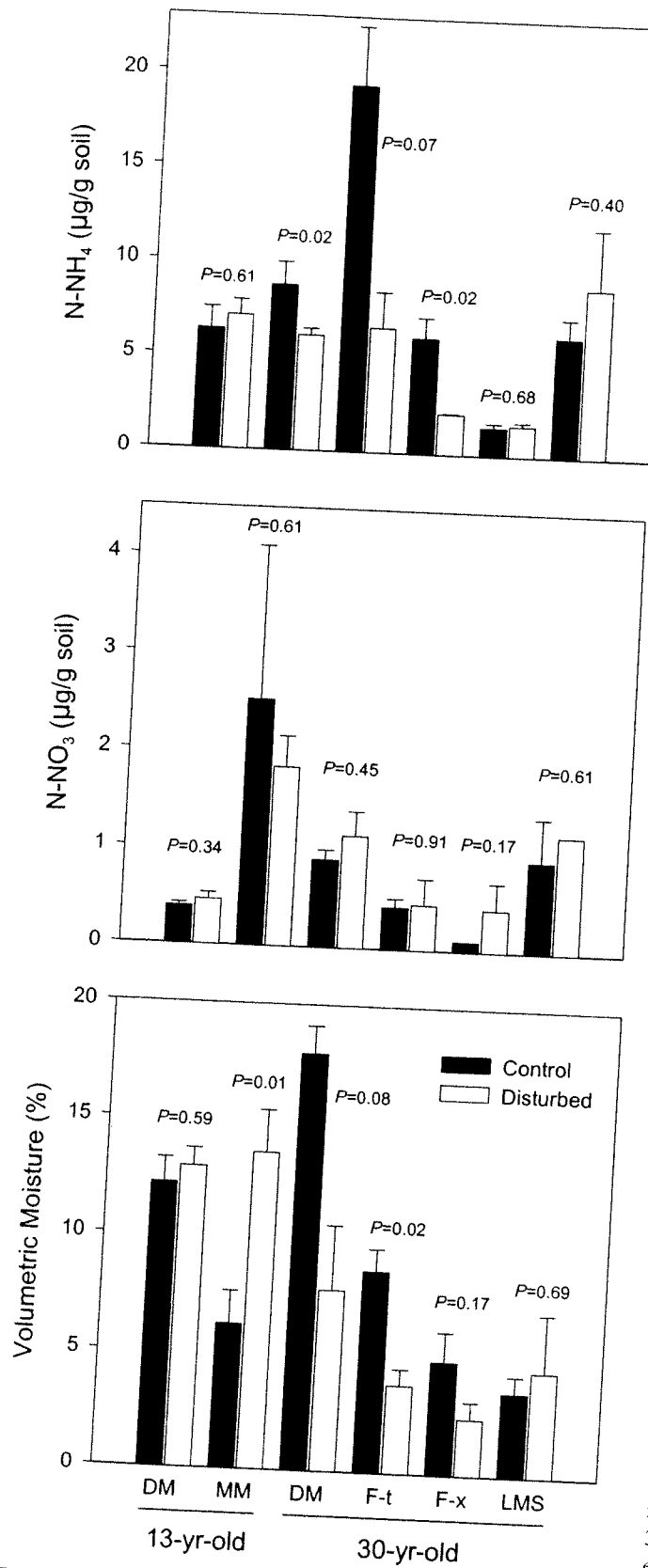
FIGURE 1. Moisture and KCl-extractable nitrogen ($\bar{x} \pm SE$; n varies, see text) in disturbed and control plots by community. Moisture was measured 4–6 August 1994, and samples were taken for nitrogen late July to early August 1994. DM = dry meadow, MM = moist meadow, F-t = typical fellfield, F-x = xeric fellfield, LMS = late-melting snowbank.

and 30-yr-old plots: 27% of species show significant differences in the 13-yr-old plots versus only 4% in the 30-yr-old plots.

However, even with the quite powerful statistical tests on the 13-yr-old plots, the generalization of few differences in relative abundance between control and disturbed plots holds (Tables 1, 2). Furthermore, there are almost no species exclusively found only in disturbed or only in control plots. Only one species, the hemiparasite *Castilleja occidentalis*, occurs in a substantial number of communities (5 of 6 examples), but never occurs in disturbed plots (Tables 1, 2). Conversely, no species occurring in more than one community is restricted to only disturbed plots, though *Thlaspi montanum* and *Sedum lanceolatum*, which occur in only two communities, are very uncommon in control plots. All species found on disturbed sites were present in the adjacent undisturbed vegetation.

Two abundant species on Niwot Ridge showed reductions in relative frequency with disturbance but still colonized. Disturbance almost eliminated *Kobresia myosuroides*, dominant of the dry meadow, from the 13-yr-old plots and reduced its frequency by about half after 30 yr (Table 1). *Geum rossii* had lower frequency in disturbed plots in three situations and similar frequencies in the remaining three (Tables 1, 2).

Other common, widely distributed species, e.g., *Artemisia scopulorum* and *Carex rupestris*, showed essentially no differences in relative frequency due to disturbance. The vast majority of less common species also occurred with similar relative frequency in control and disturbed plots (Tables 1, 2). Grasses were not abundant colonizers and in many cases showed no differences in relative frequency between disturbed and control plots. There were no differences between control and disturbed plots for *Poa glauca* (which occurred in two communities; data not presented) and *Trisetum spicatum* (three communities). *Deschampsia caespitosa* showed no differences in two of three communities in which it occurred, while the uncommon *Poa alpina* occurred only in disturbed plots of the dry meadow. Both *D. caespitosa* and *P. alpina* had very low relative frequency ($<2\%$) in the two situations where they were relatively more abundant in disturbed plots (Tables 1, 2). *Festuca brachyphylla* was the only grass to show higher relative frequency in disturbed plots in more than one community, although there were no differences in two other communities (Tables 1, 2). It also was the only grass with significant differences to have more than minimal relative frequency in disturbed plots. However, its cover was very small because it occurred only as numerous, very small seedlings.

Even species with relative frequencies significantly higher in control plots invariably colonize (Tables 1, 2). An especially important example is *Kobresia myosuroides*. In the 13-yr-old dry meadow plots (Table 1), its cover comes primarily from vegetative expansion from plot edges. However, in the 30-yr-old plots (Table 1) several seedlings occurred (*Ebersole 434* @COLO, verified M. Fritts), the first seedlings recorded in the Southern Rocky Mountains for this widespread and dominant alpine species.

Cover of vascular plants after both 13 and 30 yr of recovery is generally lower in disturbed plots than in control plots (Table 3). In one of the three communities without significant differences, lack of statistical significance seems to be due to small sample size and corresponding low statistical power. Visually, 30-yr-old disturbed xeric fellfield plots show obvious reductions in vascular cover from control plots. Apparently one large individual of *Calamagrostis purpurascens* in one disturbed plot obscures this difference (control plot vascular plant covers 10%, 15%, 25%; disturbed plots 1%, 2%, 12%). The similarity in

TABLE 1

Relative frequencies[a] (%, mean ± SD) in the dry meadow and fellfield communities

	Dry meadow, 13-yr-old			Dry meadow, 30-yr-old			Fellfield—typical, 30-yr-old			Fellfield—xeric, 30-yr-old		
n	Control 8	Disturbed 8	P[b]	Control 2	Disturbed 2	P[b]	Control 3	Disturbed 3	P[b]	Control 3	Disturbed 3	P[b]
Forbs												
Arenaria fendleri	0.6 ± 1.3	1.4 ± 1.6	0.25		1.5 ± 0.8	0.12	4.1 ± 0.6	1.8 ± 1.5	0.07	2.9 ± 2.5	3.2 ± 4.0	0.93
Artemisia scopulorum	1.8 ± 2.1	1.5 ± 1.8	0.77				10.4 ± 1.9	1.3 ± 1.4	0.00 C	4.0 ± 3.0	15.0 ± 17.0	0.33
Campanula uniflora	2.9 ± 3.0	1.3 ± 2.0	0.22		1.0 ± 1.4	0.42					1.0 ± 0.9	0.12
Castilleja occidentalis	0.1 ± 0.4		0.33									
Draba sp. 1	0.3 ± 0.5	5.0 ± 6.8	0.07				1.0 ± 0.9		0.13	0.4 ± 0.8		0.38
Erigeron pinnatisectus							0.6 ± 0.6	3.1 ± 4.4	0.38			
Erigeron simplex	1.4 ± 1.2	1.7 ± 1.3	0.64				3.9 ± 3.8	3.5 ± 3.0	0.91	3.9 ± 3.9	10.8 ± 7.8	0.25
Eritrichium nanum var. *aretioides*	0.8 ± 1.4	1.7 ± 1.7	0.25				0.4 ± 0.7	0.4 ± 0.7	1.00			
Geum rossii	5.4 ± 2.9	2.2 ± 2.9	0.05 C	3.7 ± 3.8	7.2 ± 10.2	0.42	2.9 ± 2.6	0.9 ± 1.5	0.30	4.2 ± 1.0	0.4 ± 0.8	0.01 C
Minuartia obtusiloba	2.7 ± 1.0	8.0 ± 6.1	0.03 D		15.2 ± 11.1	0.31	2.8 ± 1.9	2.1 ± 2.6	0.74	4.9 ± 2.0	0.4 ± 0.8	0.02 C
Oreoxis alpina	5.0 ± 5.7	8.8 ± 8.5	0.31	19.3 ± 1.5	7.8 ± 9.7	0.19	11.0 ± 0.6	17.5 ± 5.9	0.13	7.3 ± 1.2	5.7 ± 4.2	0.56
Paronychia pulvinata						0.24	0.4 ± 0.7		0.37	3.1 ± 5.4	3.5 ± 2.0	0.91
Phlox sibirica	0.1 ± 0.3	0.2 ± 0.6	0.69	2.6 ± 0.4	3.0 ± 0.2	0.34	6.9 ± 2.2	3.9 ± 1.1	0.10	3.1 ± 1.7	5.8 ± 5.1	0.45
Polygonum bistortoides	0.1 ± 0.3	0.2 ± 0.4	0.80	3.0 ± 1.4	1.5 ± 0.8	0.35	2.9 ± 2.1	2.2 ± 2.8	0.75	10.5 ± 1.1	12.0 ± 10.4	0.81
Polygonum vivipara	11.3 ± 8.2	9.2 ± 4.8	0.54	0.5 ± 0.7	7.4 ± 4.5	0.16	0.2 ± 0.3		0.37			
Silene acaulis	1.2 ± 1.8	1.1 ± 1.3	0.86									
Tetraneuris acaulis	1.7 ± 2.0		0.03 C				6.0 ± 3.4	0.9 ± 1.5	0.07	2.0 ± 2.0	0.4 ± 0.8	0.27
Thlaspi montanum	1.6 ± 1.8	7.3 ± 3.5	0.00 D				0.4 ± 0.7		0.37	10.9 ± 0.8	8.4 ± 2.8	0.21
Tonestus pygmaeus					1.0 ± 1.4	0.42						
Trifolium dasyphyllum	1.1 ± 3.1		0.33	11.1 ± 10.2	12.1 ± 17.1	0.95	10.4 ± 1.7	18.4 ± 4.4	0.04 D	7.4 ± 1.9	9.6 ± 9.2	0.70
Trifolium nanum	0.1 ± 0.3	0.2 ± 0.4	0.86		1.9 ± 2.7	0.42	2.2 ± 2.8		0.25			
Trifolium parryi	1.3 ± 3.4	2.7 ± 7.6	0.65	8.3 ± 11.7		0.42	0.4 ± 0.7		0.37	0.7 ± 1.2	0.9 ± 1.5	0.85
Graminoids												
Carex rupestris	16.9 ± 5.1	13.0 ± 8.6	0.30	18.4 ± 1.4	21.8 ± 5.0	0.46	11.3 ± 1.1	6.9 ± 6.0	0.28	9.7 ± 1.9	6.8 ± 2.6	0.20
Deschampsia caespitosa		1.1 ± 1.4	0.04 D									
Festuca brachyphylla	0.8 ± 1.3	10.0 ± 5.0	0.00 D				6.9 ± 3.1		0.37			
Kobresia myosuroides	24.2 ± 5.3	0.6 ± 0.8	0.00 C	21.1 ± 1.8	11.1 ± 0.7	0.02 C		14.8 ± 13.3	0.37			
Luzula spicata	0.1 ± 0.3		0.33				2.4 ± 2.1	10.3 ± 5.0	0.06		0.9 ± 1.5	0.37
Poa alpina		1.2 ± 1.5	0.03 D									
Trisetum spicatum	0.1 ± 0.3	0.4 ± 0.7	0.37	0.8 ± 1.1		0.42						
Other												
Lloydia serotina	7.7 ± 6.7	12.2 ± 8.2	0.25	5.3 ± 0.80	1.1 ± 1.5	0.07		7.2 ± 12.5	1.00	5.5 ± 3.6	7.9 ± 3.2	0.42
Selaginella densa	9.2 ± 3.6	1.4 ± 1.6	0.00 C	1.0 ± 1.4		0.42	9.6 ± 3.3	0.9 ± 1.6	0.02 C	14.6 ± 3.6	3.2 ± 4.0	0.02 C

[a] Rare species not shown (species occurring in ≤2 communities, with maximum cover <5%, and without significant differences between means).

[b] From t-tests as described in the text. Letters indicate means higher in control (C) or disturbed (D) plots.

TABLE 2

Relative frequencies[a] (%, mean ± SD) in the wet meadow and late-melting snowbank communities

n	Wet meadow, 13-yr-old				Late-melting snowbank, 30-yr-old		
	Control 8	Disturbed 8	P[b]		Control 2	Disturbed 2	P[b]
Forbs							
Arenaria fendleri							
Artemisia scopulorum	5.5 ± 4.8	2.0 ± 3.0	0.10		2.6 ± 2.5	1.4 ± 1.9	0.59
Castilleja occidentalis	0.1 ± 0.3		0.33		3.8 ± 1.2	19.7 ± 18.0	0.19
Draba sp. 1					1.0 ± 1.7		0.50
Erigeron simplex	4.1 ± 5.2	1.3 ± 2.1	0.18			2.7 ± 3.8	0.27
Geum rossii	29.8 ± 9.1	13.7 ± 7.7	0.00 C		7.1 ± 7.2	7.0 ± 1.5	0.98
Minuartia obtusiloba	2.2 ± 3.3	4.7 ± 7.3	0.41		12.5 ± 5.6	7.9 ± 4.1	0.40
Polygonum bistortoides	9.6 ± 6.2	18.5 ± 18.2	0.21		8.6 ± 8.5	4.5 ± 6.3	0.61
Ranunculus adoneus	0.7 ± 1.1	1.9 ± 5.4	0.55		2.6 ± 2.0	3.0 ± 4.2	0.90
Sibbaldia procumbens	3.7 ± 4.1	12.1 ± 9.6	0.04 D		11.3 ± 4.4	4.8 ± 3.0	0.17
Trifolium nanum		0.2 ± 0.5	0.33		16.3 ± 7.3	5.0 ± 7.0	0.18
Trifolium parryi						10.8 ± 15.3	0.27
Graminoids							
Deschampsia caespitosa	41.5 ± 19.1	29.2 ± 27.8	0.32		19.4 ± 6.1	13.7 ± 15.6	0.59
Festuca brachyphylla	2.5 ± 3.0	14.5 ± 6.4	0.00 D		4.9 ± 0.9	7.1 ± 2.5	0.22
Luzula spicata					2.5 ± 2.5	3.3 ± 0.9	0.69
Trisetum spicatum					5.0 ± 3.7	4.8 ± 3.0	0.97
					0.3 ± 0.6	1.4 ± 1.9	0.41

[a] Rare species are not shown (species occurring in ≤2 communities, with maximum cover <5%, and without significant differences between means).
[b] From *t*-tests as described in the text. Letters indicate means higher in control (C) or disturbed (D) plots.

mean vascular plant cover between control and disturbed plots in the late-melting snowbank community is judged real. Large variations in vascular cover of disturbed plots in the 30-yr-old dry meadow (30%, 85%) makes it unclear whether cover is different from the control plot (95%). Lichen cover, in communities with more than minimal lichen cover in controls, is generally lower in disturbed plots. Bryophytes have very low cover in both control and disturbed plots.

Communities with high levels of natural disturbance regained vascular plant cover more rapidly than those with less disturbance. Soil disturbed by northern pocket gophers (*Thomomys talpoides*) covers *ca.* one-third of the late-melting snowbanks and *ca.* 10% of the moist meadow, the two communities showing the most vascular plant recovery (Table 3). The other communities investigated show only a few percent pocket gopher disturbance (Thorn, 1982).

Rates of recovery increased with moisture. Nonsnowbank communities regained vascular cover in the same order as soil moisture, dry meadow > typical fellfield > xeric fellfield (Fig. 1, Table 3). I excluded snowbank communities in this comparison, since they are wet to moist during snowmelt, but become dry after snow disappears (May and Webber, 1982; Seastedt, 2001).

Discussion

SOIL MOISTURE

Measurements reported here reflect the early August sampling date, several weeks after all snow affecting the plots had melted. Since seasonal variation and comparisons among communities are reported elsewhere (May and Webber, 1982; Taylor and Seastedt, 1994; Seastedt, 2001), only differences caused by disturbance are discussed here.

Two factors appear to affect soil moisture differences between control and disturbed plots: amount of soil organic matter

TABLE 3

Aerial cover (%, mean ± SD) of control (C) and disturbed plots (D) by growth form

Community	*n*		Bryophytes			Lichens			Vascular plants		
	C	D	Control	Disturbed	P[a]	Control	Disturbed	P[a]	Control	Disturbed	P[a]
13-yr-old plots											
Dry meadow	8	8	0.4 ± 0.7	2.0 ± 1.6	0.06	19 ± 14.8	5 ± 4.6	0.04	72 ± 10.0	14 ± 6.8	0.000
Moist meadow	8	8	0.0 ± 0.0	0.02 ± 0.07	0.35	0.4 ± 1.0	0.01 ± 0.04	0.32	81 ± 13.4[b]	26 ± 7.3	0.000
30-yr-old plots											
Dry meadow	2	2	0.0 ± 0.0	0.05 ± 0.07	0.42	2 ± 2.8	21 ± 26.9	0.42	95[c]	58 ± 38.9	0.99
Fellfield—typical	3	3	0.1 ± 0.1	0.0 ± 0.0	0.16	4 ± 2.5	2 ± 0.0	0.24	70 ± 5.0	10 ± 8.5	0.000
Fellfield—xeric	3	3	0.0 ± 0.0	0.0 ± 0.0	1.00	28 ± 11.6	8 ± 2.9	0.04	17 ± 7.6	5 ± 6.1	0.10
Late-melting snowbank	3	2	0.0 ± 0.0	0.0 ± 0.0	1.00	0.3 ± 0.6	0.05 ± 0.07	0.51	75 ± 26.0	45 ± 28.3	0.32

[a] P values from paired *t*-tests (13-yr-old plots) or random groups *t*-tests (30-yr-old plots).
[b] *n* = 7; one photo unavailable.
[c] *n* = 1; one photo unavailable; *t*-test for single observation compared to group.

and differing abilities of plant species to control stomatal conductance. In the 30-yr-old dry meadow, removal of the thick organic horizon (Seastedt, 2001) reduced water storage capacity, and soil moisture dropped by more than half (Fig. 1). However, cleared areas with intact organic horizons in this community have moister soils than controls due to transpiration losses from intact vegetation (Theodose and Bowman, 1997). Species in dry alpine sites reduce water losses to minimal amounts under dry conditions while species from moister areas continue to transpire at moderate rates (Ehleringer and Miller, 1975; Oberbauer and Billings, 1981). Thus, transpiration losses in control plots in the 13-yr-old moist meadow may have reduced soil moisture relative to disturbed plots. In the 30-yr-old fellfield plots, strong stomatal control may have minimized water loss from control plots. Unshaded disturbed fellfield plots lost more water presumably due to strong insolation, one of the main controls on evapotranspiration on Niwot Ridge (Isard, 1986; Isard and Belding, 1989). In the xeric fellfield and late-melting snowbank communities, disturbed and control plots had roughly similar vegetation cover (Table 1) and apparently similar, low amounts of organic matter. These factors likely led to the similar soil moistures.

In communities with dry soils by the end of the growing season (Fig. 1), reduced soil moisture likely lowers seedling survival and growth rates. Colonization of disturbances in moister communities could tend to be more rapid unless disturbed areas were wet enough in autumn for needle ice to heave seedlings (Heidmann, 1976).

SOIL NITROGEN

The August nitrate and ammonium values for controls are indistinguishable from July measurements in the same Niwot Ridge plant communities (Bowman et al., 1993). Although pools of extractable nitrogen at one time do not equate to nitrogen availability through the season, it seems likely disturbed plots in three of six comparisons (Fig. 1) have less available nitrogen than control plots. Naturally revegetating sites in Montana's Beartooth Mountains also had somewhat lower extractable nitrate and ammonium to controls (Chambers et al., 1987).

In nitrogen-limited systems such as Niwot Ridge (Bowman et al., 1993; Bowman and Fisk, 2001), low available soil nitrogen overall and lower concentrations in some disturbed areas may slow seedling establishment and colonization of disturbed sites. Chambers et al. (1990) and Chambers (1993) found that seedlings of alpine plants in low nitrogen environments grew more slowly than those in high nitrogen situations. Seedlings with shorter and/or smaller roots would be more susceptible to drought and to heaving by needle ice (Heidmann, 1976). Low levels of nitrogen would also not favor grasses, which respond favorably to high nitrogen levels (Bowman et al., 1995; Chambers, 1997).

VEGETATION RECOVERY

Even after three decades, plant cover reestablishes slowly on small, denuded alpine areas on Niwot Ridge (Table 3), as others have found in the Front Range (Rocky Mountain Park: Willard and Marr, 1971; Greller, 1974; Pikes Peak: Ebersole, pers. obs.). Only in the late-melting snowbank community, where ongoing natural disturbance of pocket gophers has apparently selected for species that vegetatively colonize small, disturbed areas readily, does cover return to control values within 30 yr. Probable seedlings from a number of species were observed, but subjectively the vast majority of cover came via veg-

etative expansion from plot edges. Larger anthropogenic disturbances would recover even more slowly due to reduced vegetative expansion from edges. Differences in species composition between these small disturbances and larger disturbances might also occur.

Lack of seeds does not likely limit recovery in these communities. Moderate-sized seed banks exist in several Rocky Mountain alpine communities (Archibold, 1984; Chambers, 1993; Humphries, 1993), so seed banks probably exist under communities studied here. However, the most common species in the dry meadow seed bank on Niwot Ridge, *Androsace septentrionalis, Silene acaulis, Poa glauca, Minuartia obtusiloba,* and *M. rubella* (Humphries, 1993), are not abundant on disturbances in this community (Table 1). Seed rain almost certainly does not limit seedling density, based on data from other alpine sites (Chambers, 1993; Urbanska et al., 1999; Urbanska and Fattorini, 2000). Presence of seedlings in several undisturbed communities and gopher mounds greater than 5 yr old on Niwot Ridge (T. Forbis, unpub. data) also indicate that seeds are available in this environment.

Seed capture does not likely limit reproduction by seed in these commentates since gravelly surfaces (Chambers, 1991; e.g., fellfields and late-melting snowbanks) or areas with litter (Nelson and Chew, 1977; e.g., moist meadow) trap seeds well. Only parts of the 13-yr-old disturbed dry meadow plots are smooth organic surfaces, and seeds probably frequently blow out of the plots.

Seedlings on disturbed Niwot Ridge plots likely survive poorly, and this contributes greatly to slow colonization. Seedling survival was very low on the Beartooth Plateau in soil with particles greater than 1 to 2 mm (Chambers, 1995), and survival of seedlings on bare soil of gopher mounds was lower than in undisturbed vegetation on Niwot Ridge (T. Forbis, unpub. data).

While *K. myosuroides* commonly produces seedlings in the Arctic (Walker, 1990), Osburn (1958) and Bell and Bliss (1979; *K. bellardii* = *K. myosuroides*) reported a total absence of its seedlings in the Southern Rocky Mountains. It also did not occur in seed banks of the dry meadow on Niwot Ridge (Humphries, 1993). Bell and Bliss (1979) concluded *K. myosuroides* did not reproduce by seed at present though apparently it did in two cooler times in the last ca. 200 yr. The several seedlings found in this study occurred in an unusual microsite, a small (50 × 50 cm) area ca. 10 cm below the surrounding undisturbed tundra. These depressions probably collected a large number of *Kobresia* seeds over 30 yr since depressions in windy deserts capture many more seeds than flat areas (Reichman, 1984). Occasional *Kobresia* seeds with mature embryos (Bell and Bliss, 1979) would probably be deposited there. The 30-yr interval since disturbance may have included better conditions for *Kobresia* seed development, as seed viability of alpine plants shows strong variation among years (Chambers, 1989). Seedlings of *K. myosuroides* are probably quite rare and will not contribute significantly to recovery on larger disturbances in the dry meadow. However, we now know that viable seeds are produced in at least some years and that seedlings can survive the current climate in at least some exceptional conditions.

Recovery at this alpine site follows Whittaker's (1974) and MacMahon's (1980) generalizations that succession is less obvious in alpine areas than in most other terrestrial ecosystems. These alpine communities on Niwot Ridge do not show distinct groups of colonizing species versus species of mature vegetation. They do not follow the sequential replacement of species described by the relay floristics model (Egler, 1954) or the facilitation model (Connell and Slatyer, 1977). Essentially all vascular

species act as both colonizers and as components of the mature vegetation, and the majority are even present in similar relative frequencies in control and disturbed plots. The one species present in control plots but never occurring as a colonizer, *Castilleja occidentalis*, is a partial root parasite (Harrington, 1954), which may explain its difficulty in colonizing.

Other alpine areas also show poorly defined changes in species composition through recovery. On Pikes Peak in the Colorado Front Range disturbances recover very slowly and do not have a distinct suite of early colonizing species (pers. obs.). Gibson and Kirkpatrick (1992) found a lack of serial replacement of species in a Tasmanian alpine cushion heath community. Roxburgh et al. (1988) noted lack of species restricted to the pioneer role in a disturbed New Zealand alpine cushionfield after 11 yr, although one grass species was much more abundant in disturbed sites than in controls. In Rocky Mountain Park, Greller (1974) found slow recovery on roadcuts, with one grass species more abundant than any other colonizer. In lichen heath in the Caucasus Mountains species composition changed little through 15 yr of recovery and was similar to control areas. Graminoids were somewhat more abundant via vegetative sprouting from plants remaining after this partial disturbance (Onipchenko and Golikov, 1996). In the Olympic Mountains Bell and Bliss (1973) found very slow recovery on road cuts and road fills after 31 yr except on the stable, moister foot of the fill slope. A mixture of grasses and forbs colonized; some species of each type were both more and less abundant than in undisturbed areas.

On Montana's Beartooth Plateau, several grass species are distinct early successional species, and even large disturbances regain plant cover relatively rapidly. A 0.5-ha, 35-yr-old borrow pit had ca. 25% cover (Chambers, 1993), much more than expected on disturbances of similar size and age in the Front Range. Grasses, especially *Deschampsia caespitosa* and *Trisetum spicatum*, dominated many disturbed sites with a variety of soils and climates (Chambers et al., 1984). On the 35-yr-old borrow pit, grasses comprised 76% of the cover, and only grass species had greater than 1% absolute cover (Chambers, 1993). However, on a highway construction disturbance, two species of *Carex*, *Sibbaldia procumbens*, and *Cerastium beeringianum* dominated (Chambers et al., 1984).

These alpine recovery studies support the statements by Whittaker (1974) and MacMahon (1980) that alpine communities do not exhibit well-defined successional sequences. Some sites exhibit extremely limited differences in relative amounts of various species through recovery (Bell and Bliss, 1973; Gibson and Kirkpatrick, 1992; this study). At other sites almost all species from the undisturbed vegetation colonize disturbances, but one or more grass species increase in relative abundance compared to undisturbed sites (Greller, 1974; Chambers et al., 1984; Roxburgh et al., 1988; Chambers, 1993). Differences in soil moisture and soil nitrogen possibly explain these differences, but many studies do not report them. However, a grass species is a dominant colonizer of roadcuts in Rocky Mountain Park (Greller, 1974) while on the geographically close and very similar Niwot Ridge, grasses are not more abundant in disturbances. Grasses commonly respond positively to increased nitrogen, but extractable nitrogen on the grassy Beartooth Plateau borrow pit (Chambers, 1993) was even less than in this study. It seems more likely that local site differences and varying ecologies of certain species control whether grasses are relatively more abundant during recovery of alpine sites.

IMPLICATIONS FOR MANAGEMENT

Given the slow recovery of the alpine vegetation investigated, it is extremely important in similar, and probably all, al-

pine ecosystems to avoid losing plant cover. Disturbances substantially larger than the maximum 1-m^2 areas studied here will recover even more slowly due to minimal vegetative expansion from plot sides. Based on data from this study, small disturbances in late-melting snowbanks may recover within several decades without restoration efforts if further disturbance is prevented. However, if disturbed snowbank communities have even moderate slopes, they should be revegetated since soil erosion is much greater in snowbank communities than in other Niwot Ridge vegetation types (Bovis and Thorn, 1981). Small disturbances in wet sedge meadows may also recover reasonably quickly without further disturbance, based on data from the Arctic, where species of the same genera dominate very similar sites (Ebersole, 1987; Forbes et al., 2001). However, most recreationally disturbed alpine sites in Colorado occur in drier communities (Conlin and Ebersole, 2001; Ebersole et al., 2002). Due to very slow recovery in these drier communities, even small disturbances will require active restoration to prevent soil erosion and return a plant cover to the sites.

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